EFFECTS OF INCREASED SNOW ON GROWTH AND ALLOCATION PATTERNS OF ARCTIC PLANTS

By

Claire E. Addis

RECOMMENDED:

Dr. Roger W. Ruess

Dr. Donald A. Walker

Dr. M. Syndonia Bret-Harte, Advisory Committee Chair

Dr. Diane Wagner, Chair, Department of Biology

APPROVED:

Dr. Paul W. Layer
Dean, College of Natural Science and Mathematics

Dr. John C. Eichelberger
Dean of the Graduate School

4/25/14

Date

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Claire E. Addis, B.A.

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ABSTRACT

While summer warming in the Arctic has led to an increase in shrub cover on the tundra, winter processes may enhance shrub growth. In particular, greater snow accumulation around shrub patches may alter plant growth by insulating soil and facilitating overwinter nitrogen mineralization by microbes, thereby increasing nutrients available to plants at spring thaw and influencing growth patterns. We used three snow fences located across a gradient of shrub height and density at Toolik Field Station to compare plant growth and nutrient uptake on either side of the fences. Species behaved individualistically, with some showing increased growth and nutrient uptake with snow addition, others showing decreased growth and nutrient uptake, and some showing no effect of snow. The biggest increases in growth were seen in the deciduous shrub *Salix pulchra* due to increased carbon allocation (compared to nitrogen allocation) to stems, coinciding with increases in secondary growth, which allowed plants to support more branches and thus more leaves. Overall, secondary growth was the most responsive growth trait to snow addition, and facilitated growth of other aboveground plant parts. This provides a preliminary mechanistic explanation for the widespread increase in shrub cover across the northern latitudes. Some species, notably the evergreen shrub *Ledum palustre,* showed decreased growth under snow addition, but increased nitrogen uptake in stems suggesting storage of nutrients over growth. In addition, species growing in inherently more productive areas responded most strongly to added snow, indicating that larger plants are better able to modify their biomass and nutrient allocation in response to environmental alteration. We conclude that faster-growing species with the ability to respond rapidly to changes in nutrient availability will likely dominate under continued climate change, and may alter important ecosystem processes such as carbon and nitrogen storage and potentially feed back into climate warming.

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Chapter 1

GENERAL INTRODUCTION

Climate change and shrub expansion in the Arctic

The arctic regions of the world are unique because plant life is restricted by extreme conditions found few other places: a relatively short growing season, large temperature and light fluctuations between seasons, and a limited nutrient supply. Because of these limitations, the arctic is more vulnerable than most other ecosystems to global climate change (Serreze et al. 2000). Slight alterations in temperature and precipitation have the potential to drastically alter vegetative growing regimes and may cause feedbacks for climate change.

In the arctic, climate change is occurring more rapidly than elsewhere; indeed arctic air temperatures are rising faster than in other parts of the world at a rate of 0.5°C per decade, whereas overall global air temperatures are rising at a rate of 0.05-0.075°C per decade (Serreze et al. 2000, 2007, Kaufman et al. 2009). Sea ice decline and poleward transport of heat and moisture are likely causes for this amplified warming in the Arctic (Alexeev et al. 2005, Serreze and Barry 2011). Arctic warming has also coincided with increased productivity across the tundra (Walker et al. 1993, Myneni et al. 1997, Jia et al. 2003, Bhatt et al. 2010, 2013), notably in the southern Arctic due to increased shrub cover, which has been observed in arctic Alaska and also across the Arctic (Arft et al. 1999, Sturm et al. 2001b, Tape et al. 2006, Blok et al. 2011a, 2011b, Frost and Epstein 2013). A widely accepted explanation behind this trend is that warmer temperatures accelerate summer growth (Sturm et al. 2005); indeed, several studies have linked increased radial and shoot growth with warmer temperatures (Hallinger et al. 2010, Blok et al. 2011a, Myers-Smith et al. 2011).

Shrub expansion in the Arctic has also been attributed to environmental alterations such as disturbance or changing nutrient regimes that favor shrub growth. Several species in particular are increasing in abundance across the Arctic, among them

birches (*Betula* spp*),* willows (*Salix* spp), and alder (*Alnus* spp), all of which are fast-growing, making them better able to respond to changing conditions (Myers-Smith et al. 2011). With increasing disturbance in the Arctic, such as tundra fires, permafrost thaw, and thermokarst formation, new sites are becoming available for recruitment and colonization (Frost et al. 2013, Bret-Harte et al. 2013) and shrubs have taken advantage of the absence of competitors and increased in abundance near such disturbances (Schuur et al. 2007, Frost et al. 2013). Changing nutrient regimes may also favor shrub growth, as they are able to quickly translate increased nutrient availability into increased growth (Chapin 1980), shown often in fertilization studies (Shaver and Chapin, III 1980, Chapin et al. 1995, Chapin and Shaver 1996, Bret-Harte et al. 2002).

Snow-vegetation interactions

Another component of climate change that may potentially favor shrub growth is predicted increases in winter precipitation, which will likely result in greater snow depths (Maxwell 1992). In arctic and alpine environments, snow is a prominent part of landscape for a substantial part of the year, and the relationship between snow and vegetation has been studied extensively in these environments.

Early snow augmentation studies in the San Juan Mountains of southwestern Colorado quickly identified snow as a controlling factor of alpine vegetation, primarily by shortening the growing season during which plants must photosynthesize and reproduce (Spencer 1975, Webber et al. 1976). The distribution of snow varies over the landscape, with some areas likely to receive more snow than others. For example, exposed ridges typically accumulate very little snow, which indicates that effects of increased snow will also vary with the landscape. Spencer (1975) predicted that increased snow cover may cause a re-distribution of plant community types, as different plant communities exist according to winter snow regimes, and may threaten species unique to typically snow-free habitats. While many plants can exist within a range of environmental conditions, it has been shown that plants have optimal snow depths where they occur abundantly, indicating that snow controls their distribution (Walker et al. 1993, 2001).

The amount of snow accumulation is an important factor dictating the length of the growing season. In the alpine, snowpack is generally deeper and more heterogeneous due to variable topography, ranging from deep semi-permanent snowbanks to dry, wind-blown ridges with little snow accumulation whereas arctic tundra snow may be wind-hardened and thin, with drifts forming due to microtopographic features (Walker et al. 2001). Areas accumulating more snow over the course of the winter typically experience later-melt out which has been shown to delay phenological events such as greenup, flowering and seed set. In the Arctic, snow addition by snow fences delayed melt-out by two weeks compared to areas of ambient snowfall, decreasing the effective growing season, but did not affect the rate of phenological development (Borner 2006, Borner et al. 2008). In areas that are snow-free for a relatively short period of time annually, a shorter growing season by only a few weeks could significantly diminish opportunities for growth.

Besides controlling the length of the growing season and thus the timing phenological events, snow affects vegetation in a variety of ways, including modifying site hydrology, increasing winter soil temperatures and protecting plants from wind and frost damage (Jones et al. 2001). Perhaps the largest contribution of snow to the surrounding plant community is water input at spring melt-out. Snow greatly affects water availability and overall site moisture and may be the single most important factor controlling biomass production. Indeed normalized difference of vegetation index (NDVI), or greenness, is correlated to soil moisture and thus snow depth (Walker et al. 1993, 2001), indicating plant growth is positively affected by snow. In the Arctic, areas of moderate snow depth and high site moisture support larger shrubs and fewer graminoids and understory species, while areas of deepest snow support only the most snow-tolerant species like small evergreen shrubs or prostrate deciduous shrubs (i.e. *Dryas octopelata, Cassiope tetragona, Salix reticulata*)(Borner 2006). Vigorous shrub growth in the Arctic is linked to moderate to deep winter snow cover and high site moisture (Ebersole 1985, Komarkova and McKendrick 1988), indicating there may be a tradeoff between beneficial snow moisture inputs and snow deep enough to significantly

shorten the growing season and limit productivity; this provides further evidence that plants have an optimal snow depth at which they occur most abundantly. Similarly in alpine environments, areas that support lush shrub growth are typically located downslope from semipermanent snowbanks, thus receiving large water and nutrient inputs from flowing melt-water, but are snow-free long enough sustain significant growth (Walker et al. 2001). Both the location and depth of snowbanks shape the plant communities around them, thus altered snow regimes will necessarily affect vegetation patterns.

In addition to supplying water and nutrients to plants, snow also protects plants against harsh winter conditions, such as abrasive wind and frost damage from freezing conditions (Jones et al. 2001, Sturm et al. 2001a). Indeed, shrub height has been shown to correspond to snow height, with low survival of buds protruding above snow level due to abrasion by snow and ice (Ebersole 1985). Snow also ameliorates harsh winter soil temperatures because of one vital property of snow: its ability to act as an insulator. Snow drifts insulate the soil below, resulting in warmer soil temperatures (Jones et al. 2001, Sturm et al. 2001a, 2001b, Walker et al. 2001), frequently documented by snow fence experiments, though drifts produced by snow fences are deeper than is expected due to increases in winter precipitation in the near future. Warmer soils allow microbial activity to persist during the winter when it would otherwise diminish, facilitating higher rates of nitrogen (N) mineralization than would otherwise occur (Schimel et al. 2004, Sturm et al. 2005). Coupled with warmer soil temperatures is a deepening of the active layer as permafrost thaws. A deeper active layer results in increased availability of soil nutrients, as microbes gain access to and degrade previously frozen organic matter (Schuur et al. 2008, Nowinski et al. 2010). Thus deeper snow has the potential to influence plant growth by making more nutrients available for plant uptake in two ways, increased overwinter N mineralization and increased degradation of organic material.

Plant community response to snow addition

The effect of increased snow on arctic and alpine tundra ecosystems has been the subject of much previous study. Several studies focus on community and ecosystem-level responses and document changes in community composition under increased snow; in arctic ecosystems woody shrubs tend to increase, while graminoids, lichens and bryophyte abundance generally decrease, as does overall species diversity (Wahren et al. 2005, Wipf and Rixen 2010). Alpine tundra ecosystems also show reductions in species richness in response to enhanced snowpack (Seastedt and Vaccaro 2001). In addition, canopy height increases in response to snow, primarily due to increased growth of deciduous shrubs (Sturm et al. 2001b, Wahren et al. 2005) , which display more flexible growth responses than evergreen shrubs and other growth forms (Shaver and Kummerow 1992). Several studies have also documented increased ecosystem and soil respiration due to warmer soil temperatures from snow insulation (Schimel et al. 2004, Nobrega and Grogan 2007, Morgner et al. 2010), likely from increased microbial activity. Increased winter respiration rates may alter ecosystem carbon balance, with the potential to shift ecosystems from being a carbon (C) sink to a C source (Nobrega and Grogan 2007, Morgner et al. 2010).

These observations have important implications for potential global climate change feedbacks. Shrub expansion will likely perpetuate a loop of soil warming and increased respiration. As shrub abundance and canopy height increase with warming, shrubs may be better able to trap snow blowing across the tundra, leading to drift accumulation and warmer soils. As a result, the active layer deepens and wintertime microbial activity is increased, thus more nutrients are made available for plant uptake. This allows for increased growth and further shrub expansion, completing the feedback loop (Sturm et al. 2001a, 2005, Wookey et al. 2009). Another potential feedback to climate change is through albedo effects of shrub expansion. According to one hypothesis, increasing canopy height due to warming will result in taller shrubs protruding above the snow surface. Consequently, more energy will be absorbed by the dark plants at the surface, which will contribute to warming temperatures by reducing

winter albedo (Sturm et al. 2005). Warmer temperatures promote shrub expansion, thus reduced albedo creates an additional feedback to warming.

It is clear that shrubs are increasing in cover across the Arctic and that predicted increases in snowfall may perpetuate further expansion, but what is less clear is exactly how plant growth strategies may change in response to these environmental alterations that may eventually lead to shrub dominance at the expense of other growth forms. Specific growth and nutrient allocation patterns of individual species in response to snow are understudied and understanding individual plant response to altered snow regimes may help elucidate the mechanisms behind these community–level observations and better characterize predicted plant response to global warming. Since increased snow is likely to increase nutrient availability for plants, plant responses to fertilization may provide useful insight into plant responses under increased snow. In addition, as plant community composition changes under continued shrub expansion, plant-plant interactions will undoubtedly influence plant growth and survival.

Plant response to fertilization

Past studies examining plant response to fertilizer addition, primarily N and phosphorus, may be particularly useful in predicting plant response to snow addition because deeper snow will likely enhance wintertime N mineralization. Nitrogen has the greatest effect on growth of any macronutrient, as it affects the size and number of cells produced by a plant (Chapin 1980). Indeed, N fertilization has been reported to stimulate shoot growth and N concentration in newly formed tissues in tundra plant species representing three functional groups: deciduous shrubs, evergreen shrubs and graminoids, with the highest concentrations in deciduous shrubs (Shaver and Chapin 1980). Nitrogen fertilization has also been shown to affect leaf growth in varying ways: deciduous shrub *Betula nana* showed a decrease in individual leaf mass, and increase in leaf number (Shaver et al. 2001), while evergreen shrub *Ledum palustre* showed no change in leaf number, but an increase in leaf mass per shoot, likely due to increase in leaf size (Chapin and Shaver 1985). Further, graminoids (*Eriophorum vaginatum, Eriophorum angustifolium* and *Carex aquatilis)* all showed strong increases in tiller mass with

fertilization (Chapin and Shaver 1985). In general, slow-growing species (evergreen shrubs) and species with determinate leaf number (graminoids) respond to nutrient addition by increasing leaf mass and size, while fast-growing species (deciduous shrubs) produce more leaves, which are often thinner and have a higher SLA. Nomenclature for arctic species follows Hultén (1968)

In another N addition study, deciduous shrubs, most notably *B. nana*, have shown increased biomass allocation to leaf-producing shoots and structural braches, leading to a dense *B. nana* canopy at the expense of other species (Bret-Harte et al. 2001). *Betula nana* dominance in this experiment was also aided by increased secondary growth, providing support for plants to grow taller and allow for branching higher on stems, above competing species. Indeed, secondary growth accounted for a much higher proportion of net primary productivity in fertilized plots compared to ambient conditions (Shaver et al. 2001). While many studies have documented increases in stem mass and shoot growth across species from different functional groups, this rapid shift in allocation observed in this study enabled dramatic shrub expansion of *B. nana* (Bret-Harte et al. 2001, Shaver et al. 2001). It seems that in some cases, increasing the biomass of certain plant tissues may actually enhance growth of other plant parts. For example, increased branching may support increased leaf production, though this may be at the expense of reduced allocation elsewhere, likely belowground (Litton et al. 2007, Litton and Giardina 2008). The efficiency with which a plant can utilize available resources and direct it towards growth may strongly influence which species dominate an ecosystem. If plant responses to snow addition are similar to their responses to fertilization, then fast-growing shrub species will likely increase in abundance.

Plant-plant interactions

As shrubs increase in abundance they may alter the microclimate around them in such a way that may either benefit or harm surrounding plants, and this interaction may eventually determine which species will persist. Plants in every environment interact with each other and numerous studies have been conducted in effort to describe the complex relationships that exist between plants and the potential influence such

interactions may have on individual growth patterns. In some instances, close proximity of one plant to another is beneficial to at least one of the plants involved, especially under extreme or stressful environmental conditions (Brooker and Callaghan 1998). Benefit to the plant often does not come through exchange of resources, but rather because the plant benefactor ameliorates harsh external conditions that limit growth (Hunter and Aarssen 1988). For example, Carlsson & Callaghan (1991) found that *Carex bigelowii* experiences enhanced growth when sheltered by dense stands of dwarf shrubs in the Arctic. They hypothesized that the dwarf shrubs protect *C. bigelowii* from desiccation by wind and strong summer sun and likely create a warmer, moister microclimate for the plants. Any negative effects experienced by *C. bigelowii* due to competition for resources because of the species' close proximity were apparently outweighed by the benefits provided by the dwarf shrub community. Thus the balance between the opposing forces of plant competition and facilitation will determine whether the outcome of plant-plant interactions is positive or negative (Brooker and Callaghan 1998) and the interaction between tundra shrubs and nearby individuals is likely to be influential for plant growth.

There are several reasons to believe that shrub expansion in the arctic may affect growth of neighboring plants. First, as stated above, shrubs may improve unfavorable conditions by providing shelter to other plants. Second, shrub patches trap their own litter and may also collect wind-blown litter, leading to increased soil nutrient content through increased decomposition rates. Other plants growing nearby may benefit from better soil conditions (Carlsson and Callaghan 1991). Lastly, as shrubs increase in height and density, they will likely shade other species growing beneath them, creating competition for light. This may induce changes in growth patterns of shaded plants. Indeed, *C. bigelowii* produced larger leaves when shaded by dwarf shrubs (Carlsson and Callaghan 1991) and *L. palustre* produced large leaves when shaded by *B. nana* (Bret-Harte et al. 2001). While shrub density and proximity to other plants may initially enhance individual plant growth, it is likely that eventual competition for resources, such as nutrients and water, may dictate growth (Carlsson and Callaghan 1991). Under

increased snow conditions, however, greater nutrient availability may ameliorate some competition for nutrients, thus the combination of increased snow and the beneficence of plant-plant interactions may mutually enhance growth responses among co-existing plants in a given community. It is likely that pre-existing vegetation structure will influence plant response to increased snow accumulation. Study of plant allocation patterns in locations representing a gradient of shrub height and density may also help elucidate the mechanisms behind landscape change and the shrub expansion phenomenon.

Project goals

This project aims to address how plant communities may change if predicted increases in winter precipitation under continued climate change are realized. Since snow is a vital component of arctic communities, any changes to snow regimes will likely have widespread effects on the surrounding vegetation. By examining individual species' responses to added snow across several habitats, we hope to identify what changes in growth and allocation are occurring at the species level that may contribute to shrub expansion documented throughout the Arctic.

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Chapter 2

SECONDARY GROWTH MAY DRIVE SHRUB EXPANSION UNDER INCREASED SNOW IN THE ARCTIC[1]

ABSTRACT

Increased shrub cover in the Arctic has been linked with summer warming, but it is also likely winter processes may enhance shrub growth. Large shrub patches can trap snow around them, resulting in deep snow drifts. Greater snow depths may alter plant growth by insulating winter soil and facilitating overwinter nitrogen mineralization by microbes, thereby increasing nutrients available to plants at spring thaw and influencing growth patterns. We used three snow fences located across a gradient of shrub height and density at Toolik Field Station to compare plant growth on either side of the fences. We found species behaved individualistically, with some showing increased growth with snow addition, others showing decreased growth, and some showing no effect of snow. The biggest increases in growth were seen in deciduous shrubs due to increases in secondary growth which allowed plants to support more branches and thus more leaves. This provides a preliminary mechanistic explanation for the widespread increase in shrub cover across the northern latitudes. In addition, species growing in inherently more productive areas responded most strongly to added snow, indicating that larger plants are more plastic in response to environmental alteration. We conclude that faster-growing species with the ability to respond rapidly to changes in nutrient availability will likely dominate under continued climate change, resulting in further shrub expansion.

[1] Addis, C. E., & M. S. Bret-Harte. Prepared for publication in *Journal of Ecology*.

INTRODUCTION

In the arctic, climate change is occurring more rapidly than anywhere in the world (*ACIA* 2005). Indeed, arctic air temperatures are rising faster than in other parts of the world at a rate of 0.5°C per decade, whereas overall global air temperatures are rising at a rate of 0.05-0.075°C per decade (Serreze et al. 2000, 2007, Kaufman et al. 2009). This warming has led to increased tundra productivity (Myneni et al. 1997, Jia et al. 2003, Bhatt et al. 2010, 2013) likely due to increases in shrub cover, frequently observed in arctic Alaska and across the Arctic (Arft et al. 1999, Sturm et al. 2001b, Tape et al. 2006, Blok et al. 2011b, Myers-Smith et al. 2011, Frost and Epstein 2013). A widely accepted explanation behind this trend is that warmer air temperatures accelerate summer growth (Sturm et al. 2005, Blok et al. 2011b), a fact established in phytogeographic analyses across the Arctic (Alexandrova 1980, Yurtsev 1994, Walker et al. 2005), though shrub growth can show spatial and temporal variation (Blok et al. 2011a, Frost et al. 2013).

Another aspect of climate change likely to result in landscape change is increased winter precipitation, which will likely result in greater snow depths (Maxwell 1992). The ecosystem-level implications of increased snow accumulation are far-reaching, and results in a shorter snow-free period, delayed phenology of plant growth, and substantial alterations to site hydrology (Spencer 1975, Walker et al. 1993, Jones et al. 2001, Borner et al. 2008). In addition, snow insulates the soil, resulting in warmer winter soil temperatures, which allows microbial activity to persist during the winter (Walker et al. 1999, Sturm et al. 2001a, 2001b, Schimel et al. 2004, Natali et al. 2011). The snow-shrub hypothesis defined by (Sturm et al. 2001a) predicts that because wintertime microbial activity is increased by warmer soils, more nutrients will then be available for plant uptake in the spring allowing for increased growth and further shrub expansion, leading to a feedback loop as bigger shrubs can theoretically trap more snow. Indirect effects of this hypothesis include a deeper active layer, degradation of previously frozen organic matter and reduced winter albedo due to dark shrubs protruding above the snow, all of which may create addition feedbacks to warming and further shrub expansion (Sturm et

al. 2005, Chapin et al. 2005, Schuur et al. 2008, Wookey et al. 2009, Nowinski et al. 2010).

The effect of increased snow on arctic tundra ecosystems has been the subject of much previous study, but most research has focused on community and ecosystem-level responses in effort to characterize shifts in ecosystem function and species abundance, and less on plant level-changes in growth patterns. Snow fence experiments document changes in community composition leading to overall reductions in species richness, but increased growth of woody shrubs, particularly deciduous shrubs, and an associated increase in canopy height (Seastedt and Vaccaro 2001, Sturm et al. 2001b, Wahren et al. 2005, Walker et al. 2006, Wipf and Rixen 2010). While these general trends provide valuable insight into the effects of global warming on tundra plant communities, relatively little is known about the small-scale plant responses underlying these larger trends. In particular, specific growth and nutrient allocation patterns of individual species in response to snow are understudied. Many plants in the arctic grow clonally, thus changes in biomass allocation can have large effects on their abundance and cover, since many rooted 'individuals' share an underground rhizome (Bret-Harte et al. 2001). Understanding individual plant response to altered snow regimes may help identify the mechanisms behind these community–level observations and better characterize predicted plant response to global warming.

A plant's resource allocation strategy, where it chooses to invest acquired nutrients, has direct implications for productivity and nutrient storage. In addition, biomass allocation is important in the acquisition of resources, both above and below-ground via leaves and roots, and for plant architecture and support via primary and secondary growth. How a plant allocates resources to these various components determines how a plant is able to respond to changing environmental conditions, such as those predicted by global climate change (Lambers et al. 2008). As discussed above, deeper snow conditions may influence plant nutrient uptake the following spring which potentially will have different consequences for different species because growth

strategies, nutrient requirements, and nutrient allocation patterns differ considerably among plant functional groups.

Arctic plant communities include many plant functional types, but we chose to focus on the three most common ones for this study: deciduous shrubs, evergreen shrubs and graminoids (Chapin et al. 1995). In order to predict how these functional types may respond to environmental change, it is necessary to understand their growth habits. It is thought that fundamental trade-offs exist among plant traits that allow plants to either effectively capture resources or tolerate low resource availability, and that these two strategies often align with particular functional groups (Grime 1977, Komarkova and McKendrick 1988, Box 1996, Diaz et al. 2004). In general, evergreen plants are slow-growing, and are characterized by low tissue turnover and production, whereas deciduous shrubs and graminoids are fast-growing and often experience quick tissue turnover and high production (Shaver and Kummerow 1992, Diaz and Cabido 1997). Slow-growing species typically exhibit a smaller growth response to increased nutrients than faster-growing species, because they have low nutrient requirements due to slow rates of tissue production and low tissue nutrient concentrations. Instead, they are more likely to store nutrients for use during times of nutrient stress (Chapin 1980, Diaz et al. 2004). Graminoids, whose leaf number is determinate, will show a response to increased nutrient availability by changing their leaf size and tillering rate rather than leaf number, whereas deciduous shrubs with variable leaf numbers may produce more leaves which are thinner (higher specific leaf area (SLA)) in response to increased nutrient availability (Chapin 1980, Diaz and Cabido 1997, Shaver et al. 2001). Woody shrubs also have the capacity to alter biomass allocation to both primary and secondary stem growth, which accounts for a large proportion of net primary productivity in the Arctic and is sensitive to environmental alterations like nutrient addition (Shaver 1986, Bret-Harte et al. 2002). Secondary growth (wood production) in particular influences the overall plant architecture and the capacity for increased growth because of mechanical support provided by stems and branches (Campioli et al. 2012a).

While previous research has focused on the effects of fertilization on plant growth, individual plant response to increased snow depth is relatively unstudied, though especially how growth patterns differ across and within plant functional groups (deciduous shrubs, evergreen shrubs, and graminoids). Because greater snowfall may increase plant nutrient availability, it is probable that species' responses will be similar to those experienced under fertilization. Snow addition is known to affect community structure and function, but research is still needed to determine what plant-level allocation modifications are taking place that allow shrub dominance and overall canopy height to increase. Furthermore, little is known about how plant response to snow addition may differ across habitats undergoing varying stages of shrub expansion and with different initial nutrient status. Previous work indicates different factors control growth of a single species along a natural snow gradient (McGraw and Fetcher 1992), thus we expect increased snow to affect plant growth differently across different habitat types. Study of plant allocation patterns across locations representing a gradient of shrub height and density (Barkman 1988) may help elucidate the mechanisms underlying shrub expansion and landscape change.

The goal of this study was to determine what plant-level changes in aboveground biomass allocation are driving ecosystem-level responses to snow addition, how these changes may vary across tundra habitat types, and the associated implications for continued shrub expansion. We hypothesized that 1) greater snow accumulation will enhance growth of arctic plants, due to increased nutrient availability, and plant response will vary by functional group (response size: deciduous shrubs > graminoids > evergreens). We further predicted that biomass of both woody tissues (primary and secondary tissues) and leaves will increase in response to deeper snow conditions, with the greatest increase in deciduous shrubs as they can respond more quickly to altered environmental conditions than evergreen shrubs. We expected that a plant would either produce more leaves (deciduous and evergreen shrubs) or bigger leaves (graminoids) in response to deeper snow. Second, we hypothesized that 2) woody species that show the biggest increases in secondary growth will show the largest overall increases in biomass

because increased structural support can better sustain continued growth. Third, we hypothesized that 3) plants will show a greater growth response to snow addition where shrub height and density increase along a natural gradient from tussock tundra to shrub tundra. We expect that as shrub height and density increase, canopy plants will show greater increases in growth than sub-canopy plants because they are not subject to light limitation and can more efficiently utilize increased nutrients resulting from greater snow depths. Increased growth of canopy plants will be manifested in greater leaf and stem production, including secondary growth. We also expect that although growth responses will not be as great for sub-canopy plants, sub-canopy plants will also show increased growth as shrub height and density increases because their proximity to shrubs will lessen exposure to harsh conditions, and because greater nutrient availability due to increased snow depths will reduce competition for nutrients. Increased growth will be manifested in increased leaf size and potentially decreased leaf thickness (higher SLA) due to competition for light.

METHODS

Site description

This study was conducted near the Toolik Field Station (68.38°N 149.36°W), site of the Arctic Long Term Ecological Research (LTER) project located in the foothills of the North Slope of the Brooks Range, Alaska. Mean annual air temperature is approximately -10°C and mean annual precipitation is 318 mm, of which 43% falls as snow. Average ambient snow depth is 50 cm, though snow distribution is variable due to drifting from wind (DeMarco et al. 2011). In order to address our hypotheses we collected plant samples from both windward and leeward sides of experimental snow fences near Toolik Field Station.

In 2005, four snow fences were constructed near Toolik Lake in three different vegetation types: (1) low shrub (tussock tundra with a canopy height of approx. 6 cm), (2) intermediate shrub (shrub tundra with a canopy height of approx. 32 cm), and (3) tall

shrub (shrub tundra with a canopy height of approx. 55 cm) (Fig. A.1) (DeMarco et al. 2011). Arctic shrubs can grow much taller than 55 cm (Viereck et al. 1992), thus the terms tall, intermediate and low shrub used here refer to relative shrub height and are meant only to distinguish between community types. One fence was erected at each site except at the tall shrub tundra site where two shorter fences were used due to patchy distribution of tall shrubs. Fences are 1.5 m tall and 60 m long, except at the tall shrub site where there are two 30-m fences. Fences are constructed of plastic black mesh snowfencing attached to triangular wooden supports. The snow fences run east-west because winter winds come predominantly from the south; this allows for drift accumulation on the north sides of the fences. Data collected between 2006 and 2008 indicate that maximum snow depth north of the fences ranges from 1.5-1.8 m but can be less during low snow years (Bret-Harte, unpublished data). Snow depth measurements taken in spring 2012 showed a maximum accumulation of 191 cm behind the snow fences, with an average of 113.24 cm, compared to the average 71.17 cm of snow accumulation windward of the fences (Fig 2.1). Drifts of greater than 1 m can extend north of the snow fences as much as 15 m, but typically extend to 10-12 m. Drift accumulation during the winter raises soil temperatures by 6-10°C (DeMarco et al. 2011). In addition, snow drifts delay snowmelt in the spring by 8-14 days (Bret-Harte, unpublished data).

Site characterization

Canopy greenness

To provide a general description of the canopy at each site, two measurements of canopy greenness were taken along both sides of each snow fence during the first two weeks of August in 2010 and 2011: Leaf Area Index (LAI) and Normalized Difference Vegetation Index (NDVI). LAI measures the green leaf area per unit ground area. Using an optical plant canopy analyzer (LAI 2000 LI-COR Inc., Lincoln, NE), three readings were taken every 5 m along a 50 m transect on either side of the fences. Leeward transects were located within a distance of 4 m from the snow fence, where winter snow

accumulation is the greatest. Windward transects were generally located farther from the fence to avoid any effects of windward snow accumulation immediately north of the fences (Fig. A.2). For the two tall shrub sites, these measurements were taken along the 30-m length of the fences, totaling 60 m between the two fences. In the same manner, 4 readings were taken with a Unispec SC Spectral Analyzer (PP Systems, Amesbury, MA) every 5 m along the same 50 m transect on each side of the fence to determine the NDVI for each snow fence site (Fig. A.2). NDVI is a normalized ratio of the near-infrared and red bands in the light spectrum and is used to measure the photosynthetic capacity of vegetation at a given site (Jackson and Huete 1991).

Relative species abundance

In order to identify the most abundant species in each growth form, relative abundance was determined using a point-intersect method (Goodall 1952, Jonasson 1988). Four 50 m transects were set up at distances approximately 3, 5, 7, and 9 m from the snow fences on the leeward side, and farther out on the windward side, but with the same spacing. A pin one mm in diameter and one m in length was inserted into the ground every 0.5 m along each transect and the number of contacts ("hits") between each plant species and the pin as it is passed to the ground was recorded. The number of "hits" per plant species at each transect were totaled and divided by the total number of hits for all species to determine each species' relative percent cover (Table 2.1). Recorded plant species were separated into three functional groups: deciduous shrubs, evergreen shrubs and graminoids (forbs were not used in this study). Sample species for this project were determined by selecting the 2 or 3 plant species per functional group with the greatest number of hits. Selected species (Table 2.1) were harvested for growth analysis in late summer of 2010 and again 2011. Species abundance data were collected to determine which species are most common on both sides of the snow fences, and not as a detailed assessment of changes in plant community abundance and structure due to increased snow depth. Nomenclature follows Hultén (1968).

Plant growth analysis

Ramet and tiller harvest

Eight ramets (large, rooted branches) of each deciduous and evergreen shrub species were haphazardly collected from each side of the snow fence at each site during the first two weeks of August in 2010 and 2011. Haphazard collection involved walking a transect the length of the fence and stopping roughly every 10 steps to collect the nearest individual that appeared to be at least eight or nine years of age. In total 16 samples of each species were collected from each snow fence each year, eight from each side of the fence. Ramets were collected from along the entire length of each snow fence, taking care to collect within 2-10 m from the snow fence on the drift side to ensure that plants were covered by winter snow drifts. On the control side, plants were collected at least 10 m from the fence to ensure that they were in a zone of ambient snow depth. Maps (drawings) were made of each ramet collected showing the branching structure, age boundaries of the most apical eight or nine years of growth (procedure detailed below), locations of shoots and branching points, and the number of leaves per ramet (Bret-Harte et al. 2002). In the laboratory, the most apical eight or nine years of growth were analyzed for branch biomass and structure, secondary growth and leaf characteristics.

For graminoids species, eight mother-daughter tiller complexes were haphazardly collected in the same manner as described above. A mother-daughter tiller complex is defined as an individual tiller (mother) with at least 1 immature tiller (daughter) growing from the same rhizome. For tussock forming species, such as *Eriophorum vaginatum*, a wedge of the tussock was removed to ensure collection of at least one mother-daughter tiller complex. Collected specimens were transported to the laboratory for analysis. For tiller complexes of graminoids species, maps were made to show branching patterns of the mother and daughter tillers.

Woody biomass and secondary growth calculations

Stem biomass and rates of secondary growth were determined for woody species. For those species that had persistent terminal bud scars, branch ages for each ramet were determined by counting those scars, which indicate yearly growth (Shaver 1986). If bud

scars were not persistent, such as in *Betula nana*, thin cross-sections were made using a razor blade and growth rings were counted using a compound microscope, after cross-sections had been stained with 1% phloroglucinol in 20% HCl to aid ring visualization (Bret-Harte et al. 2002) (Fig. A.3). Once yearly boundaries were identified, stems segments of a given age (per ramet) were excised and pooled, and their aggregate length measured (Shaver 1986). Stem segments were dried at 60°C for 96 hours and weighed.

To quantify secondary growth of stems, we used calculations defined by (Bret-Harte et al. 2002), which allow for calculation of secondary growth before and after an environmental alteration, such as construction of a snow fence, which may influence plant growth. In general, the annual radial increment of a stem segment, assuming it is cylindrical, is determined from the relationship between the age of the stem segments and their mass per unit length (*m/l*). A complete description of the derivation of these equations is provided in (Bret-Harte et al. 2002); here we only provide a brief description of the calculations.

For each age class, the total weight of the stem segments was divided by the total length of those stem segments, generating the average mass (mg) per unit length (mm) of stem (*m/l)*. The square root of *m/l* of each age class was plotted against the age of the stem segment. The slope (α)($mg^{1/2}$ $mm^{-1/2}$ $year^{-1}$) of the relationship between the square root of *m/l* and age was determined across all age classes for plants harvested on the windward (control) sides of the fences. For plants harvested on the leeward (snow drift) side of the fences, separate slopes were calculated for stem segments formed 1) before the snow fences were constructed in 2005 and 2) after the snow fences were constructed. The average α for all ramets on each side of each fence was then calculated and used to determine the absolute radial increment per unit length (R) for each age class per ramet (mg mm^{-1} $ramet^{-1}$ $year^{-1}$):

$$R = 2\alpha^2\gamma + \alpha^2 + 2\alpha\sqrt{m/l} \qquad \text{Eqn 1}$$

where γ is the stem age minus 1.

The absolute radial increment per ramet (mg $ramet^{-1}$ $year^{-1}$) was then determined by multiplying the absolute increment/length (R) by the total stem segment length of each

age class. To calculate the total secondary growth of the entire ramet (mg ramet^{-1} year^{-1}), the absolute radial increment per age class was summed for all age classes. Finally, to calculate the relative rate of secondary growth (% year^{-1}), the total secondary growth of the ramet was divided by the sum of the masses of each age class.

Leaf characteristics

In order to determine biomass changes in leaves of woody species, leaves were removed from each ramet, and counted. Total leaf area was measured using WinRhizo image analysis software (Regent Instruments, Inc., Canada). All leaves were dried at 60°C for a minimum of 48 hours and weighed. For graminoid species, leaves per tiller were also measured for leaf area, then dried and weighed; mother and daughter tillers were treated separately. Specific leaf area (SLA, leaf area per unit mass) was calculated for each ramet and tiller by dividing leaf area by dry mass.

Statistical analysis

We used a combination of one, two and three-way analyses of variance (ANOVAs) to analyze for treatment effects for each species at each snow fence location. Vegetation type (low shrub, intermediate and tall shrub) was included as a random effect, with snow fence treatment as the fixed effect. Because sampling occurred over two years, year was included as a blocking factor. For species occurring at more than one snow fence location, an initial three-way ANOVA was run for each growth variable (General linear model (GLM) with vegetation type, treatment, and year as main effects and all possible interactions between the three factors). For species occurring at only one snow fence, an initial two-way ANOVA was run for each growth variable (GLM with treatment and year as main effects and a treatment x year interaction). If statistically significant treatment effects for any growth variable, or a significant interaction involving treatment were found, subsequent two-way (for species occurring at multiple site) and one-way (for species occurring only at one site and having a significant treatment x year interaction) ANOVAs were run to determine for which sites and years the treatment effect was significant. In this paper, we present only tables including initial results from

the two or three-way ANOVAs (depending on how many sites the species were samples from); tables containing results from two and one-way ANOVAs resulting from subsequent analyses are provided in Appendix A.

All data were transformed prior to analysis by ANOVA if necessary to achieve normality and homoscedasticity of variance. If these assumptions were not met, data were either logarithmically or rank-transformed and ANOVAs were run on the transformed data (Zar 1999). If analyses on transformed data produced a significant interaction effect, we ran individual 2-way ANOVAs because of the difficulty of interpreting interactions of rank-transformed data due to its nonlinear nature (Quinn and Keough 2002). Still, in some cases, model assumptions could not be met by transforming the data. In these cases, data were separated first by site, then by year and transformed if needed, and analyzed separately. In these instances, we were unable to test for interaction effects between factors. Most of the time separating the data by factors and transforming allowed for analysis, but if this could not be done, a non-parametric Kruskal-Wallis test was employed on ranked data to test for treatment effects. All statistical analyses were performed in JMP 4.0.2 and an alpha level of 0.05 was considered statistically significant.

RESULTS

Site description

Measurements of LAI and NDVI provided differing results in describing canopy greenness: while there was no statistically significant difference in LAI between treatments for any vegetation type ($F_{1,110}$=.1323, $p>0.05$) , NDVI showed 6% and 3.3% increases under snow addition at the low and intermediate shrub sites, respectively (low: $F_{1,78}$=23.467, $p<0.001$, intermediate: $F_{1,80}$=5.1995, $p<0.05$) (Fig. 2.2). No difference between treatments was detected in NDVI at the tall shrub site (Kruskal-Wallis, $X^2_{(1)}$=1.554, $p>0.05$)

Plant biomass

For woody species, total biomass increased with snow addition for only one of five species sampled, *S. pulchra* (Table 2.2, Fig 2.3). When total biomass was analyzed by site, this increase was most pronounced at the intermediate site, but because of a significant interaction between sampling year and treatment ($F_{1,28}$=7.4361, P<.05), we looked at years separately and found that snow enhanced total biomass 2.7-fold relative to control plants in 2011 ($F_{1,14}$=11.9954, p<0.01) but had no effect in 2010 ($F_{1,14}$=0.5848, p>0.05). Breaking apart total biomass into its contributing parts, *S. pulchra* biomass increased significantly under snow addition in old stems, new stems and leaves (Table 2.2, Fig. 2.3). For old stems, further analysis of site and year indicated this increase was driven by plants at the intermediate site ($F_{1,28}$=12.3787, p<0.01) in 2011 only ($F_{1,14}$=13.4406, p<0.01), which showed a 3-fold increase in old stem biomass. Across sites, new stem biomass could not be transformed to meet model assumptions of homogeneity of variance, so sites were analyzed separately. New stem biomass was enhanced 2-fold by snow at both the low and intermediate sites (low: $F_{1,28}$=6.7846, p<0.05), intermediate: $F_{1,28}$=7.6719, p<0.01, Fig. 1.3), but was unaffected at the tall site ($F_{1,28}$=2316, p>0.05). Leaf biomass was also enhanced by snow (Table 2.2, Fig. 2.3); broken down by site, this roughly 2-fold increase was only apparent at the intermediate and tall sites (intermediate: $F_{1,28}$=10.388, p<0.01, tall: $F_{1,28}$=7.57, p<0.05).

None of the other species showed increased total biomass with added snow (Tables 2.2, 2.3, Fig. 2.3). In fact, in contrast to *S. pulchra*, *L. palustre* showed a 2.2-fold decrease in new stem biomass under snow addition, but there was a significant interaction between sampling year and treatment, so we analyzed years separately and found that this decrease was driven by samples collected in 2010 ($F_{1,14}$=17.266, p=0.001). There was no change in either old stem or leaf biomass of *L. palustre* (Table 2.3, Fig. 2.3). *Betula nana*, *V. uliginosum*, and *V. vitis-idaea* showed no significant difference in any components of biomass due to snow addition (Tables 2.2, 2.3, Fig. 2.3).

For graminoid species, total mass per tiller increased with snow addition in two of the four graminoids sampled (Tables 2.4, 2.5, Fig. 2.4). Total mass per tiller of *E.*

vaginatum increased 1.5- fold under snow addition, and total mass per tiller of *E. angustifolium* also increased, but only in 2010; initial analysis indicated a significant interaction between sampling year and treatment (Table 2.4), driven by a 1.4-fold increase in 2010 at the intermediate site ($F_{1,14}$=6.94, p<0.05). *Carex bigelowii* and *A. latifolia* did not change mass per tiller under snow addition (Tables 2.4, 2.5, Fig. 2.4).

Across species occurring at multiple sites, biomass generally increased from low shrub to tall shrub sites, except for *C. bigelowii*, where there was no effect of vegetation type on mass/tiller. In some cases, biomass was not statistically different between intermediate and tall sites, though an increasing trend was seen from the intermediate to the tall site (Figs. 2.3, 2.4, Tables 2.2, 2.4).

Plant architecture

To address changes in plant architecture due to snow addition in woody species, we looked at two components of plant growth: branching and secondary growth in stems. Again, woody species responded individualistically to snow addition. *Salix pulchra* responded positively for both growth components; branching and secondary growth both increased significantly under snow addition (Table 2.6, Fig. 2.5). Overall, branching rate increased over time, and snow increased the number of branches produced by the plant at both the intermediate and tall sites, 1.7 and 1.5 fold, respectively (intermediate: $F_{1,28}$=15.3741, p<0.001, tall: $F_{1,28}$=4.7533, p<0.05). There was a significant interaction between sampling year and treatment ($F_{1,28}$=5.7125, p<0.05) for the intermediate site however, and analyzing years separately revealed the increase in branching due to snow was driven by a 2-fold increase seen in 2011($F_{1,14}$=11.8429, p<0.01). The rate of secondary growth was enhanced by snow (Table 2.6), but further analyses revealed this was only at the intermediate site ($F_{1,28}$=15.9064, p<0.001) and only in 2010 ($F_{1,14}$=14.3553, p<0.01); secondary growth was actually suppressed by snow at the low site ($F_{1,28}$=8.6836, p<0.01)(Fig. 2.6).

In contrast to *S. pulchra, L. palustre* experienced negative effects of snow addition in terms of plant architecture. Indeed, branching and secondary growth were both suppressed significantly under snow addition (Table 2.7, Figs. 2.5, 2.6), 1-fold and

2-fold, respectively. The other woody species, *B. nana, V. vitis-idaea* and *V. uliginosum,* all showed no significant change in branching with increased snow (though all showed increased branching over time), but both *B. nana* and *V. uliginosum* showed decreased secondary growth with snow addition (Tables 2.6, 2.7, Figs. 2.5, 2.6). For *B. nana*, the overall decrease in secondary growth was driven by its response at the intermediate shrub site ($F_{1,28}$= 9.3895, $p<0.01$). Though *V. vitis-idaea* showed decreased branching, it did show significantly increased secondary growth under snow addition (Table 2.7, Fig. 2.6).

For graminoids, we considered the number of tillers produced to address changes in plant architecture. We did not analyze the number of tillers for *E. angustifolium* because it rarely produces more than a single tiller. Of the three other species sampled, none showed any change in tiller production under snow addition (Table 2.4).

Across species occurring at multiple sites, branching or number of tillers and secondary growth rate generally increased from low shrub to tall shrub sites, except for *C. bigelowii*, which produced more tillers at the low site than at either the intermediate or tall sites. Again, in some cases, branching and secondary growth rate were not statistically different between intermediate and tall sites, though an increasing trend was seen from the intermediate to the tall site (Figs. 2.5, 2.6, Tables 2.4, 2.6).

Leaf characteristics

Salix pulchra and *E. vaginatum* were the only species whose leaf characteristics responded to snow addition; all other species showed no difference in the number of leaves produced, or leaf area between snow and control treatments (Tables 2.4, 2.5, 2.6, 2.7, Figs 2.7, 2.8). *Salix pulchra* showed a significant near doubling in both leaf number and total leaf area under increased snow (Table 2.6); two-way ANOVAs revealed these increases occurred at both intermediate and tall sites (intermediate: leaf number, $F_{1,28}$=16.367, $p<0.001$, leaf area, $F_{1,28}$=15.683, $p<0.001$, tall: leaf number, $F_{1,28}$=5.8821, $p<0.05$, leaf area, $F_{1,28}$=4.438, $p<0.05$) . *Eriophorum vaginatum* showed a 1.6-fold increase in leaf area under snow conditions (Table 2.5, Fig. 2.8). No species showed a difference in SLA due to treatment (Table 2.5).

Across species occurring at multiple sites, the number of leaves and leaf area generally increased from low shrub to tall shrub sites, except for *C. bigelowii*, which showed no change in leaf area from low to tall sites (number of leaves was not analyzed for graminoids). Similar to other growth traits measured, number of leaves and leaf area were not always statistically different between intermediate and tall sites, though an increasing trend was seen from the intermediate to the tall site (Figs. 2.7, 2.8, Tables 2.4, 2.6). For two species, SLA was different among sites: for *S. pulchra,* SLA was lower at the low and intermediate sites than at the tall site, and for *C. bigelowii*, SLA was lower at the low and tall sites than at the intermediate site (Tables 2.4, 2.6).

DISCUSSION

Secondary growth may facilitate overall growth

The most striking results were the changes in secondary growth due to snow addition seen in all of the woody species included in this study. While secondary growth did not show consistent increases among species (some showed decreased secondary growth with added snow), it appeared to be the most responsive growth trait to snow addition of those measured. Though frequently overlooked in past studies of Arctic plants, Shaver (1986) first identified secondary growth as a significant proportion of aboveground production, which has been corroborated by more recent studies (Bret-Harte et al. 2002, Campioli et al. 2012b). Our results show that changes in annual rates of secondary stem growth with snow addition are comparable with those documented by (Bret-Harte et al. 2002, Campioli et al. 2012b), sometimes increasing by 40-50% (Fig. 2.6). Both Bret-Harte et al. (2002) and Campioli et al. (2012b) detected strong increases due to fertilization, indicating that secondary growth (and possibly other plant traits) are just as responsive to environmental alterations associated with increased snow as they are to fertilization. Indeed, previous work, in the Arctic and elsewhere, has also shown positive correlations between increased radial growth and snow depth (Poore et al. 2009, Hallinger et al. 2010).

For a plant to increase in size, assimilated carbon (C) must be invested in new growth (Lambers et al. 2008). If a plant can produce more branches, and thereby increase its light interception capability, more C can be assimilated via photosynthesis, which can then be allocated towards growth, likely toward secondary growth to provide mechanical support for continued growth (Campioli et al. 2012a). Increased branching will likely further lead to increases in leaf production, which may promote increased secondary growth as water transport needs will be greater, necessitating the formation of more water-conducting tracheids in the stem and increasing radial growth (Uggla et al. 1998). In addition, the concentration of indole-3-acetic acid, a plant hormone necessary for growth, is greatest in young leaf buds and shoots and may help coordinate increased cambial growth with increased apical growth (Uggla et al. 1998).

Viewed in the light of Grime's theory of competition (1977), it is likely these interrelated increases in growth of different plant parts lead to the competitive dominance of *S. pulchra.* Grime states that if a plant has both the ability to effectively capture resources necessary for growth and a high relative growth rate, then all parts of the plant will get bigger; there isn't necessarily a trade-off between growth of certain aboveground plant parts, rather the increase of one part facilitates the increase of another. Here, resource capture through increased leaf production may have fueled increased branching, primary growth and notably, secondary growth, which is necessary for mechanical support of all other increases in biomass.

Another consideration, however, is that increased aboveground growth may come at the cost of decreased partitioning to belowground structures. Partitioning of gross primary production to wood is known to increase globally in forests in response to fertilization; in fact, wood aboveground net primary production and total belowground C flux are typically inversely related in forest ecosystems (Litton et al. 2007, Litton and Giardina 2008). Since wood requires less nitrogen (N) to produce and has lower respiration rates than other plant tissues (Chapin 1989, Litton et al. 2007), the cost of producing and maintaining wood is fairly low, and it may be that increases in secondary growth, and subsequently branching and leaf production, were enabled by declines in

partitioning belowground, which we did not measure. Though relatively few studies have included calculating secondary growth as a way of measuring a plants' response to an environmental alteration, we argue that increasing secondary growth may be an important and effective way a plant can increase its size over a relatively short amount of time, as it enables increased growth of other plant parts (branches, leaves), even if growth may be reduced belowground.

Species responded individualistically

Overall, species behaved individualistically in their growth response to snow addition; some showed increased growth with snow addition, others showed decreased growth, and some species showed no effect of snow at all. Contrary to our hypotheses, growth form was not a good predictor for species' response to snow addition, as not all species within a growth form benefited from added snow. The biggest increases in growth were seen in the deciduous shrub *Salix pulchra*, while the greatest decreases were seen in the evergreen shrub *Ledum palustre*, but not all deciduous shrubs behaved the same way, nor did all the evergreen shrubs or graminoids. These results add to the mounting support against the formerly established concept that functional types respond similarly to environmental perturbations based on a correlation between form and function (Chapin III and Shaver 1985, Shaver and Chapin, III 1986, Bret-Harte et al. 2008).

Salix pulchra experienced the most dramatic increases in growth due to snow addition of all of the species studied. In addition to increased secondary growth, it showed increases in total biomass and all of the individual components of biomass, as well as the number of branches, number of leaves and total leaf area. Since the SLA of the leaves did not change with snow addition, we assume that the increase in leaf area is solely due to the increase in leaf number, rather than a change in leaf size or thickness. In accordance with our hypothesis, it is likely that the increases in secondary growth with increased snow provided enough structural support for the plant to produce more branches, which can then support more leaves, and continued growth. Deciduous shrubs like *S. pulchra* are typically faster-growing than evergreen shrubs, and are thus able to

respond via growth more quickly to environmental alterations such as increased nutrient availability from added snow. Indeed, plants that can most efficiently capture resources and translate those resources into growth will show the largest initial response, as was seen with *S. pulchra*. The ability of deciduous shrubs to allocate biomass towards secondary growth, and subsequently other aspects of growth, over a short period of time provides a preliminary mechanistic explanation for the widespread increase in deciduous shrub cover across the northern latitudes.

Contrary to *S. pulchra*, our results indicated some species responded negatively to added snow. *Ledum palustre* showed the most significant decreases in growth; decreased secondary growth corresponded with decreases in branching and leaf production, providing further support for secondary growth influencing the extent to which other plant parts can grow, though in the opposite direction of *S. pulchra.* In addition, both *B. nana* and *V. uliginosum* each showed reductions in secondary growth, perhaps because they were outcompeted by other woody plants, but showed no other corresponding decreases in other growth traits. This may be because their response is not as strong, or will take more time to manifest. Additionally, previous work has shown that for some species secondary growth doesn't necessarily correlate with primary growth (Campioli et al. 2012a, 2012b), which may partially explain why other species (*B. nana, V. uliginosum, V. vitis-idaea*) showed only changes in secondary growth and not across a suite of growth traits. .

There are several possible reasons that significant amounts of added snow during the winter months may negatively affect plant growth. First, experimentally added snow drifts take longer to melt out than areas of ambient snowfall (Walker et al. 1999, Bowman 2000, Borner et al. 2008, Cooper et al. 2011), thus both the onset of the growing season is delayed and the total duration of the growing season is shorter than areas of ambient snowfall (Walker et al. 1999, Bowman 2000, Borner et al. 2008, Cooper et al. 2011). In terms of plant growth, this means that plants growing under ambient snow conditions are exposed to light earlier than those plants under snow drifts. Near Toolik, the ground is usually snow free by early to mid-June, when the sun's light is most

intense. Around the summer solstice is a crucial time for growth in the arctic, and plants experiencing delayed leaf expansion or green-up due to late snowmelt may not be able to take full advantage of this important photoperiod (Chapin, III and Shaver 1985, Shaver and Kummerow 1992). For plants that grow slowly such as evergreen shrubs, missing a key part of the growing season can have disproportionately large effects on growth and may explain why we saw decreases in growth in some species under added snow.

For faster-growing species, such as *B. nana,* this suppression of growth due to added snow is harder to explain, especially since growth was greatly enhanced in *S. pulchra,* the other deciduous shrub. Previous literature has shown that *B. nana* responds quickly to environmental alterations (Chapin and Shaver 1996, Bret-Harte et al. 2001, 2002, Wahren et al. 2005, Zamin and Grogan 2012), so it is curious that we did not see this response. However, the *Betula* plants in this study did show signs of pathogen infection (specific type of pathogen unknown), usually visible in significant die-back of apical branches, and re-sprouting of new branches with large leaves near the bases of old stems (Bret-Harte, unpublished data). This die-back was most pronounced at the intermediate site, where the growth response was the strongest for *S. pulchra.* Though we did not select obviously infected individuals for this study, it is possible that plants could have been infected enough to reduce growth, but show no visible signs. Die-back was more widespread on the drift side of the fence, and less common on the control side. Sturges (1989) also saw declines in plant biomass due to fungal pathogens whose activity was enhanced by both warmer temperatures beneath the snowpack and lengthened duration of snow cover. It is plausible that deeper snow protected the pathogen against harsh winter conditions when it otherwise would have diminished, or possibly died.

Strongest growth responses were seen in middle-sized plants

We initially hypothesized that growth responses would increase with increasing shrub height and density, but instead we saw the greatest response to snow addition at the intermediate shrub site, not the tall shrub site. Of the species occurring at more than one vegetation type (*C. bigelowii, E. angustifolium, B. nana, S. pulchra*), most of the significant increases due to snow were seen at the intermediate site (*E. angustifolium, S.*

pulchra), and sometimes at the tall site (*S. pulchra*), but never at the low site. Comparing these sites to natural snowbed communities, the intermediate and tall sites most resemble communities found in mid snow depth zones of natural snowbeds, which are characterized by larger shrubs, less tussock-forming graminoids and few understory species (Borner 2006). Given this community similarity, it is logical that plants at the intermediate and tall sites responded most positively to added snow.

At the low shrub site, there may have been previously existing nutrient limitation or other environmental factors preventing large growth, which explain the smaller plants found there. Small plants at this site may partition more photosynthate to root production and mycorrhizae compared with the same species at the intermediate and tall sites, which are inherently more productive areas, and may partition a greater proportion of photosynthate aboveground. Indeed, many species have demonstrated similar size-dependency of allocation according to initial plant size and nutrient availability, especially deciduous shrubs which show great plasticity in size and shape depending on nutrient availability (Müller et al. 2000, Bret-Harte et al. 2001, Campioli et al. 2012a). Even plants of the same species, but showing size variability due to habitat conditions, might respond differently to environmental alterations, such as increased nutrient availability from snow addition. Smaller plants that are investing proportionately less photosynthate into aboveground production as compared to belowground (roots and mycorrhizae) might not respond immediately by increasing stem and leaf growth, though allocation patterns may shift over time under continued nutrient addition (Müller et al. 2000). In the same scenario, larger plants already investing significant resources in aboveground growth will likely continue to do so, but may shift allocation more towards stem production (secondary growth) to support overall increased growth, as seen with *S. pulchra* at the intermediate site.

Though some increases in growth were seen at the tall site, they were not to the extent seen at the intermediate site. It is possible that the tall shrub site was not nutrient limited prior to the addition of snow, due to some difference in microtopography or environmental traits from the other sites. If this were the case, plants may not have

responded strongly to increased nutrient availability, since they were not nutrient stressed.

Conclusions and implications for shrub expansion

Our results confirm that growth of at least some fast-growing deciduous shrubs (*S. pulchra* especially*)* is greatly enhanced by increased snow. The primary mechanism for enhanced growth appears to be increased secondary growth, which provides structural support for increased branching and leaf production. Because most species in our study showed significant increases or decreases in secondary growth to snow addition, we suggest secondary growth in arctic shrubs may be fairly sensitive to environmental changes and is thus a significant way in which plants can alter biomass allocation, as has been shown in trees. In addition, species growing in inherently more productive areas responded most strongly to added snow, indicating that larger plants are better able to modify their biomass allocation in response to environmental alteration. Under continued climate change, we can expect those species which can rapidly increase their secondary growth to dominate the landscape and may alter important ecosystem processes such as C and N storage.

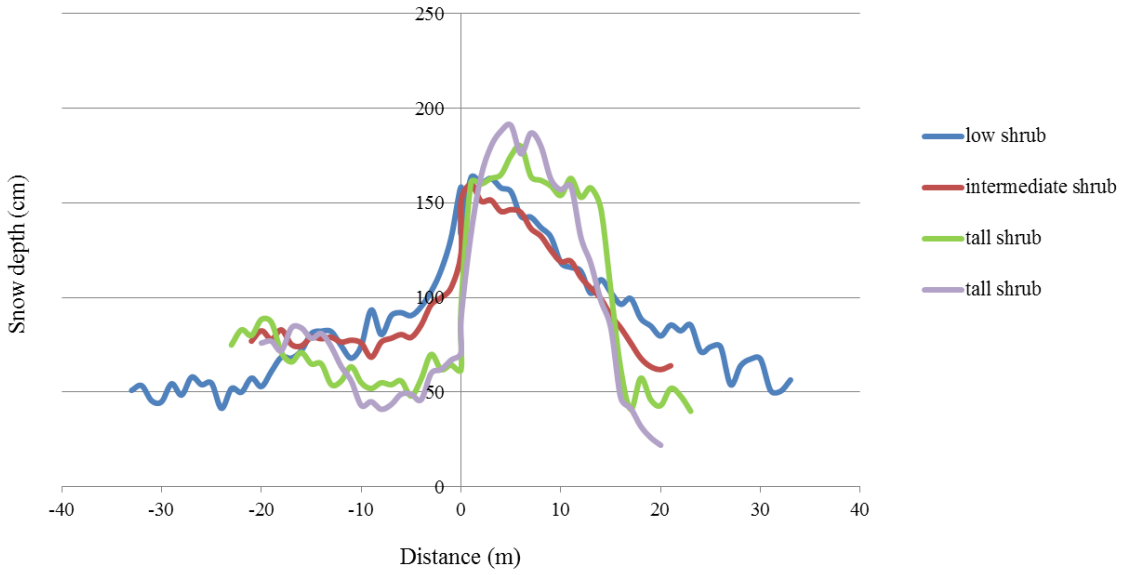

Figure 2.1 Snow depth to the south (negative distance) and north (positive distance) from each of four snow fences. Measurements are the averages from two transects per fence, made during April 2012.

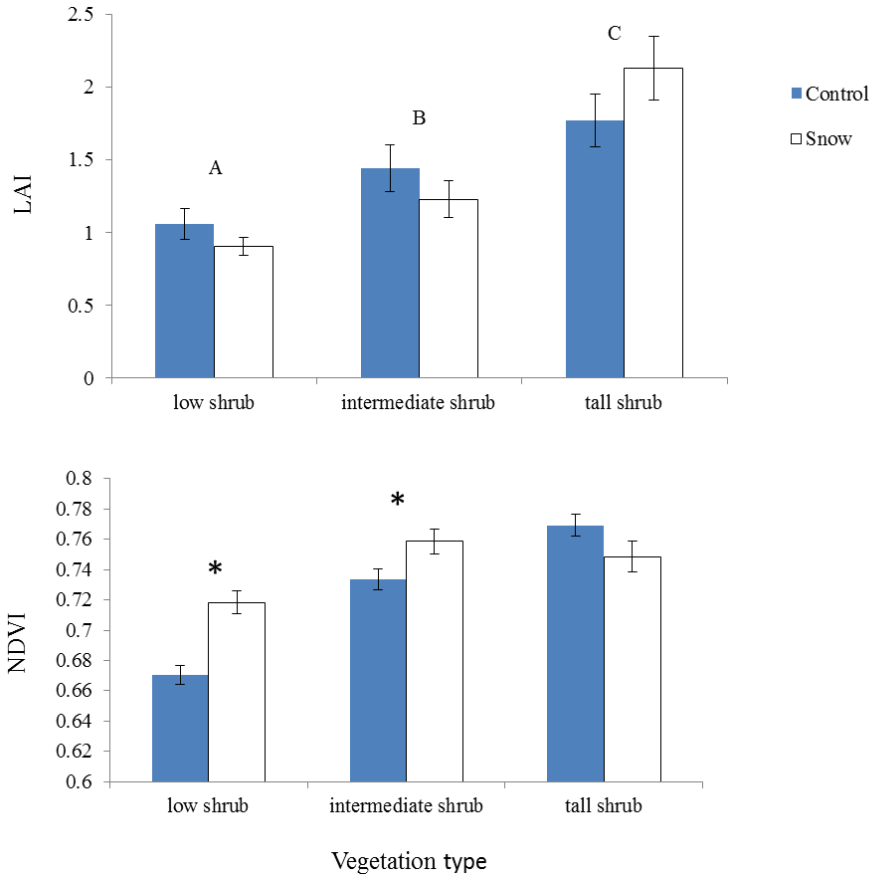

Figure 2.2 Average leaf area index (LAI)(a) and normalized difference of vegetation index (NDVI)(b) measurements at low, intermediate and tall shrub sites. Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error.

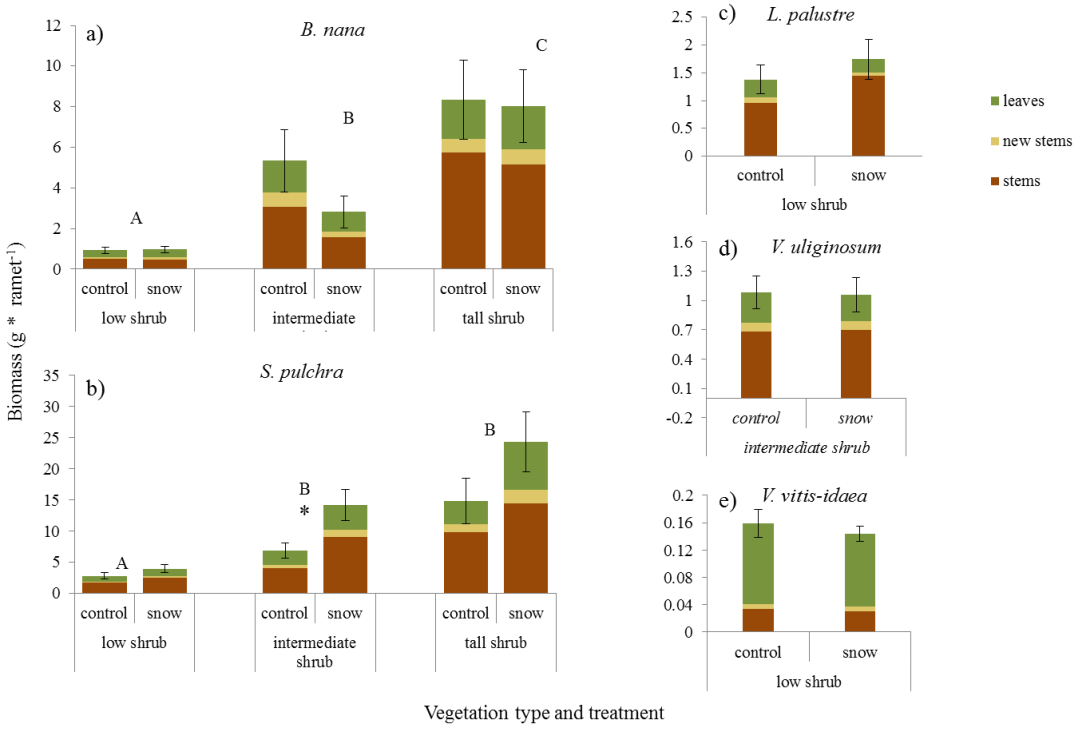

Figure 2.3 Mean biomass of deciduous shrubs (a, b, d) and evergreen shrubs (c, e). Total biomass is represented by the sum of old stems (brown), new stems (tan), and leaves (green). Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error (n=16) of the total biomass per ramet.

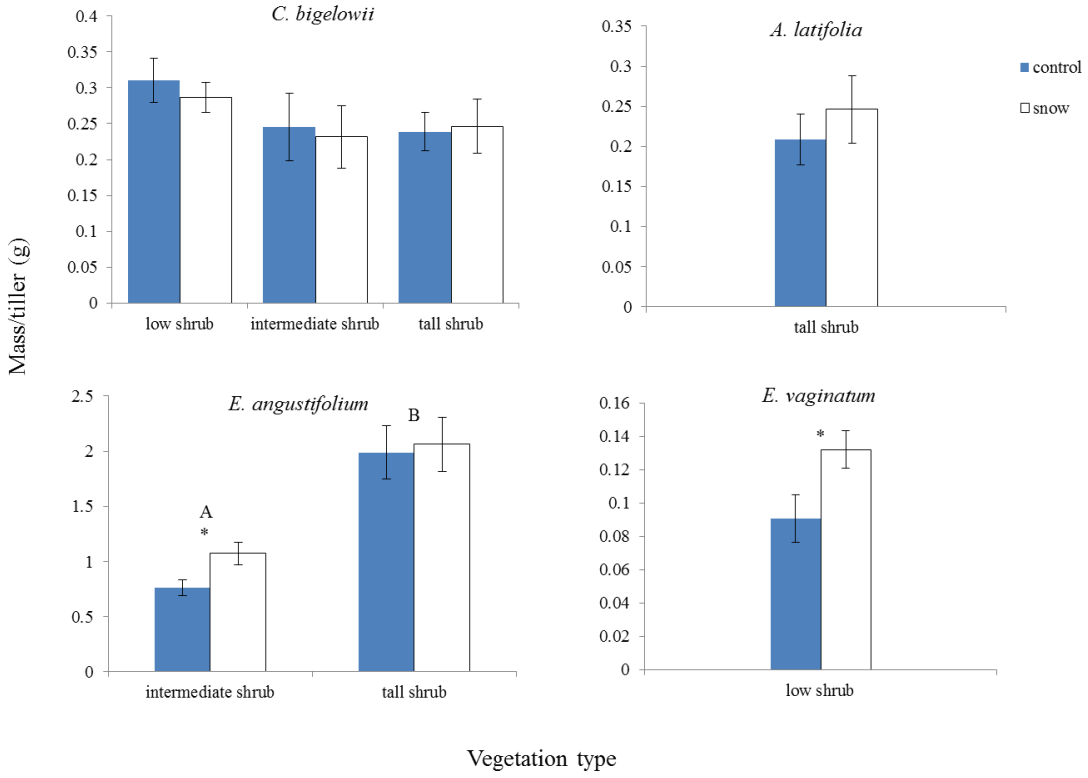

Figure 2.4 Average mass per tiller of graminoids. Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error.

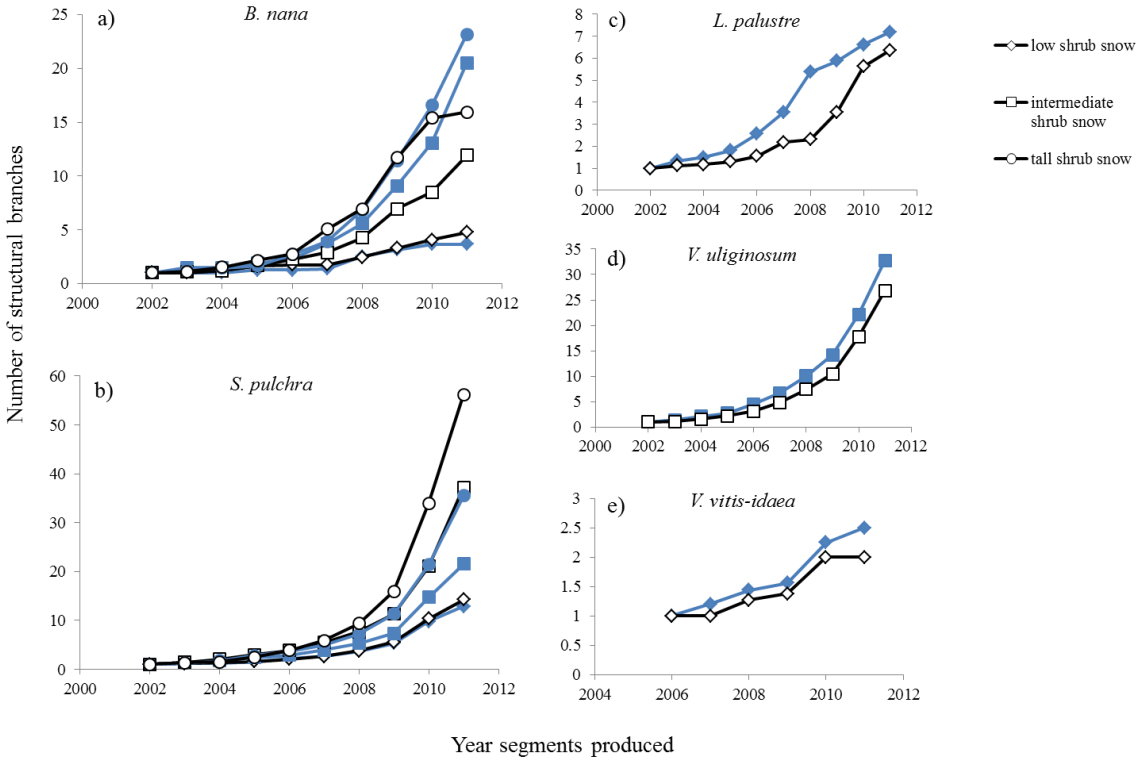

Figure 2.5 Mean number of structural branches of each age class vs. year those branches were produced for deciduous shrubs (a, b, d) and evergreen shrubs (c, e). Sites are coded by symbol shape: low shrub=diamond, intermediate shrub=square, tall shrub=circle, treatment is coded by color: blue=control, white=snow. Data were averaged over two years.

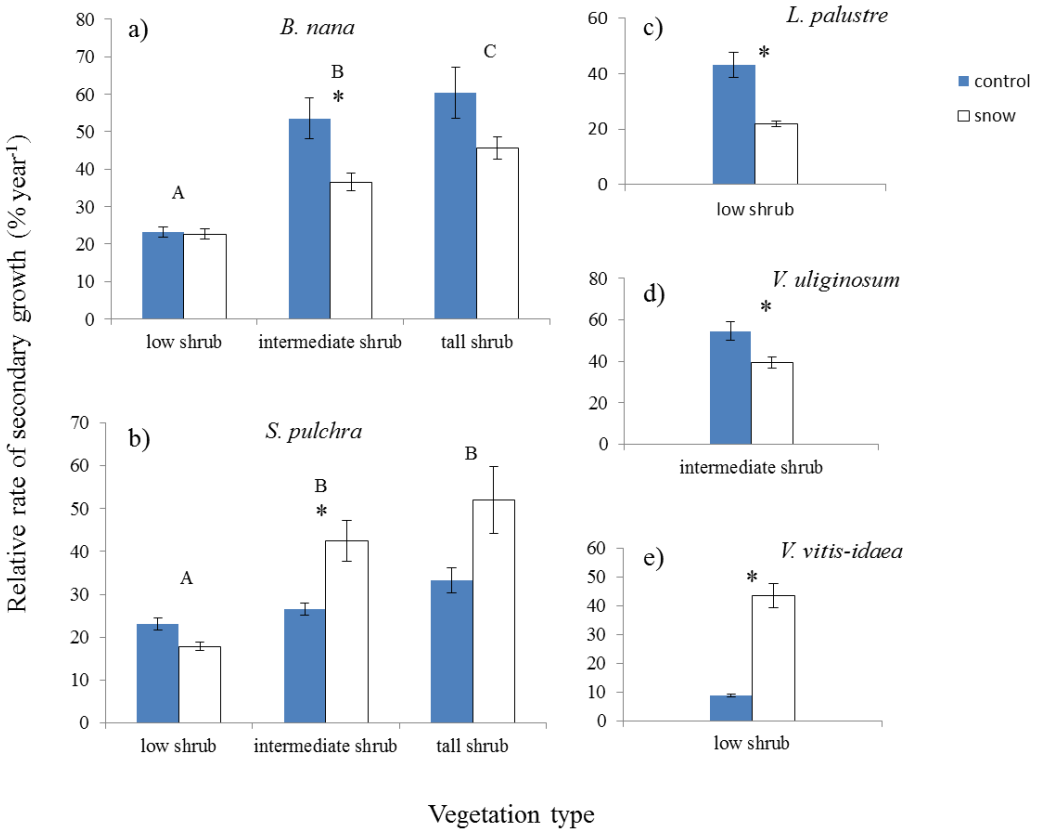

Figure 2.6 Mean relative rate of secondary growth of deciduous (a, b, d) and evergreen (c, e) shrubs. Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error (n=16).

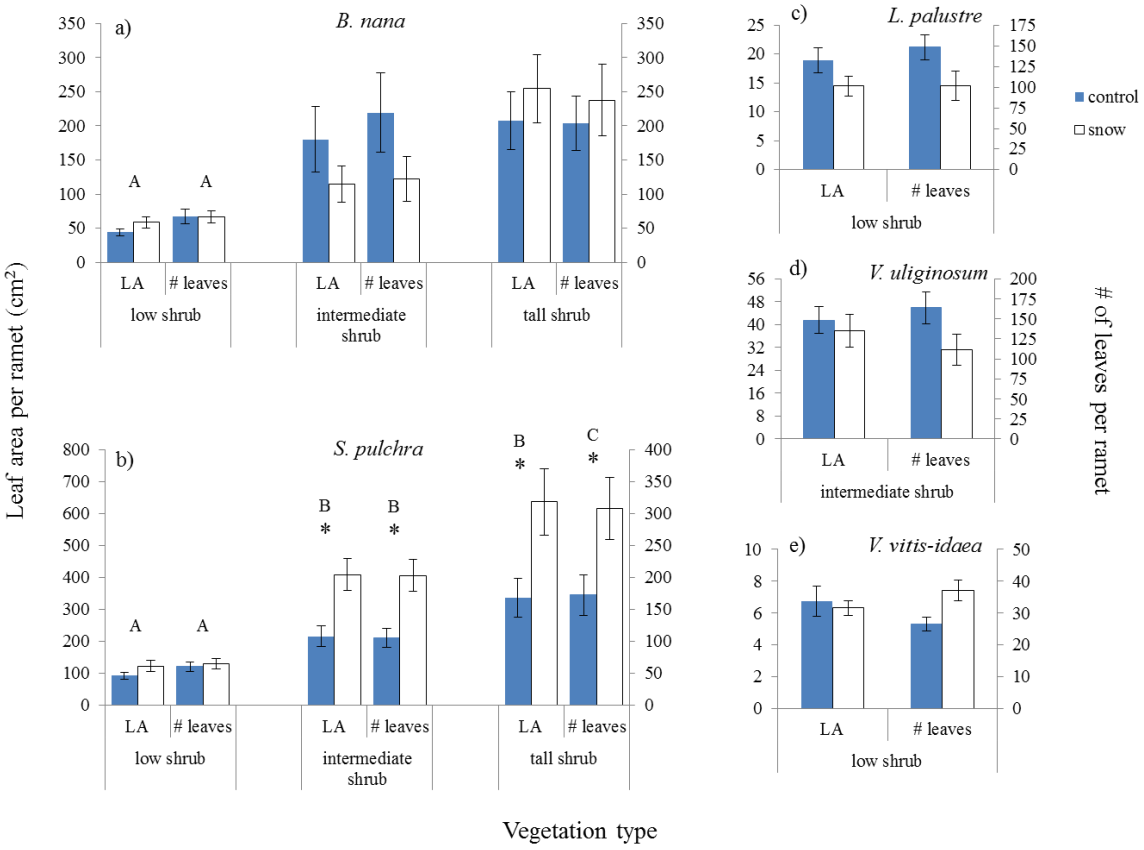

Figure 2.7 Mean total leaf area and number of leaves produced per ramet by deciduous (a, b, d) and evergreen shrubs (c, e). Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation type. Data were averaged over two years. Error bars represent ±1 standard error (n=16).

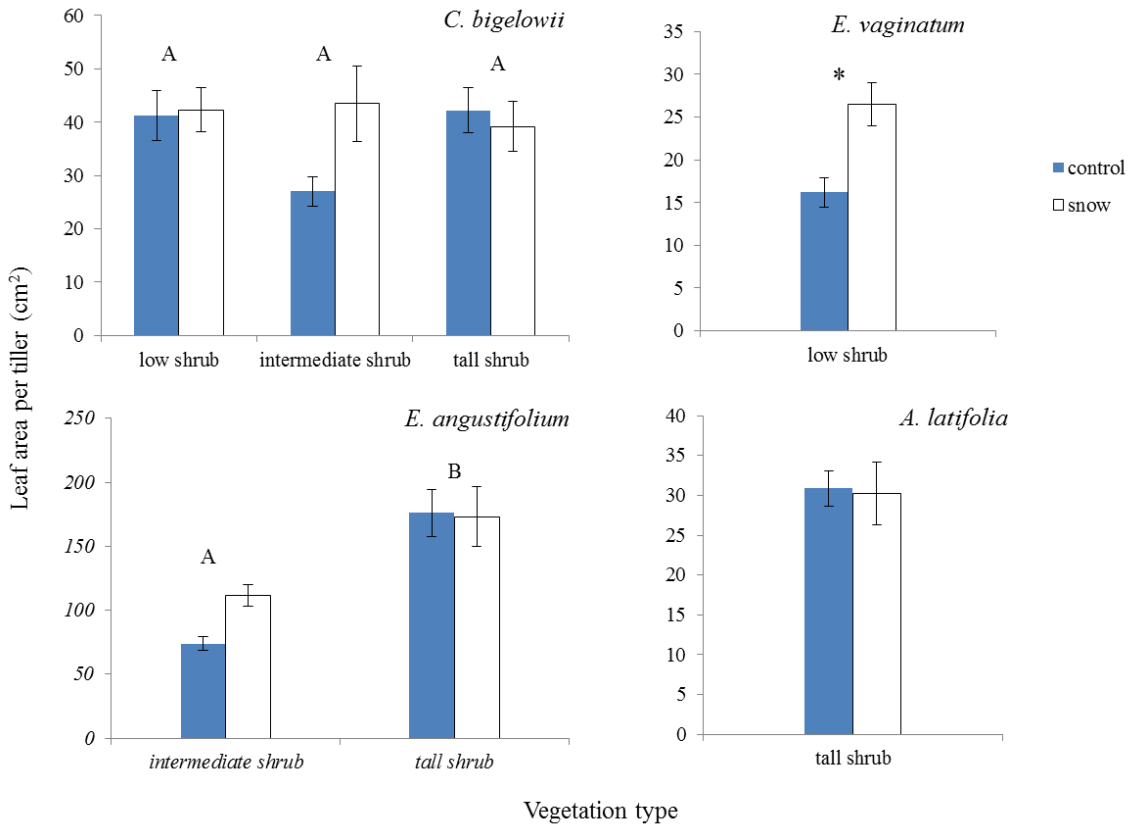

Figure 2.8 Mean total leaf area per tiller of graminoids. Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error (n=16).

Table 2.1 Calculated percent cover of plant species at each snow fence location. Species sampled at each location are shown in bold: 1= low shrub site, 2 = intermediate shrub site, 3,4 = tall shrub sites.

	Snow Fence							
	1		2		3		4	
SPECIES	control	snow	control	snow	control	snow	control	snow
Andromeda polifolia	0.38			0.35				
Arctostaphylos alpina		0.43		0.12				
Artagrostis latifolia	0.50				**35.58**	**46.00**	**6.11**	**11.25**
Artemisia arctica					0.64		0.39	0.36
Betula nana	**8.25**	**9.64**	**14.99**	**14.54**	**3.18**	**4.06**	**27.81**	**10.00**
Calamagrostis lapponica	0.64	1.63	0.25		1.91	1.74	2.56	1.79
***Carex* spp.**	**11.98**	**13.87**	**23.05**	**24.62**	**7.75**	**1.39**	**10.85**	**1.07**
Cassiope tetragona	3.74	3.47	0.00					
Dead branch	1.42	0.43	10.45	5.63	3.56	6.26	11.83	13.21
Dryas integrifolia				2.23				
Empetrum nigram	1.42	0.76	0.13	0.47		0.93		
Equisetum arvensis								0.71
Equisetum sp.			0.88	0.47			0.20	
Eriophorum angustifolium			**7.18**	**2.93**	**3.68**		**2.96**	**11.96**
Eriophorum vaginatum	**34.41**	**38.57**					0.20	
Hierchloe alpina	0.13							
Ledum palustre	**20.48**	**13.33**	0.25	0.23		1.39	0.59	
Pedicularis capitata				0.12				
Pedicularis lapponica	0.64	0.54		0.23				
Petacites frigidus					4.57	3.13	5.92	7.14
Polemonium sp.				0.47				
Polygonum bistorta	0.90	1.19	1.13	1.06		0.12	1.18	0.36
Polygonum vivaporum				0.23	0.13			
Pyrola grandiflora			0.13	0.12				
Rubus chamaemora	0.26	0.11			0.38		1.38	8.75
Salix cerrate			3.15	0.59	1.78			
Salix pulchra	**0.39**	**0.33**	**8.82**	**17.23**	**22.24**	**23.06**	**17.55**	**29.29**
Salix reticulata			2.90	3.63				
Salix unknown 1			2.39	1.99				
Sax spp.							0.20	0.71
Senecio sp.					1.02	0.46		
Stellaria longipes			0.13	0.12	0.38	0.23	2.56	0.54
unknown forb 1				0.12				
unknown forb 2				0.12				
unknown forb 3					1.52	1.27		
unknown forb 4						0.12		
unknown forb 5					0.64	0.81	0.39	
unknown forb 6	0.13			0.12				
unknown grass 1			1.76	1.41	5.08	2.55	1.58	0.71
unknown grass 2	0.13							
unknown grass 3					0.51			
unknown grass 4			0.50	0.23	0.51		0.59	0.54
unknown seedling 1				0.47				
unknown seedling 2								0.18
unknown seedling 3	0.88							
Vaccinium uliginosum	0.90	0.76	**18.26**	**18.99**		1.16	1.38	
Vaccinium vitis-idaea	**15.08**	**14.95**	0.38		0.13	0.58	3.35	0.54
Valeriana capitata			0.63	1.17	2.16	2.78	0.39	0.89

Table 2.2 Results of 3-way analysis of variance on biomass components of deciduous shrubs that occurred in multiple vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Total biomass			Old stems			New stems			Leaves		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Betula nana		(rank)			(rank)			(rank)			(rank)	
Vegetation type (V)	2, 84	**32.233*** **	**L<I<T**	2, 84	**35.771*** **	**L<I<T**	2, 84	**14.393*** **	**L<I, T**	2, 84	**27.892*** **	**L<I<T**
Treatment (T)	1, 84	0.116 ns		1, 84	0.285 ns		1, 84	0.7313 ns		1, 84	0.022 ns	
Year (Y)	1, 84	**16.581*** **	**'11>'10**	1, 84	**19.278*** **	**'11>'10**	1, 84	2.4488 ns		1, 84	**18.430*** **	**'11>'10**
V x T	2, 84	0.697 ns		2, 84	0.553 ns		2, 84	1.1769 ns		2, 84	0.6333 ns	
V x Y	2, 84	1.802 ns		2, 84	2.054 ns		2, 84	2.0696 ns		2, 84	1.5187 ns	
T x Y	1, 84	**4.023***		1, 84	3.540 ns		1, 84	1.6038 ns		1, 84	**4.523***	
V x T x Y	2, 84	1.894 ns		2, 84	1.605 ns		2, 84	0.6468 ns		2, 84	3.029 ns	
Salix pulchra		(rank)			(rank)						(rank)	
Vegetation type (V)	2, 84	**34.282*** **	**L<I, T**	2, 84	**22.310*** **	**L<I, T**				2, 84	**50.496*** **	**L<I, T**
Treatment (T)	1, 84	**11.762*** **	**S>C**	1, 84	**6.666***	**S>C**				1, 84	**16.2481*** **	**S>C**
Year (Y)	1, 84	1.0441 ns		1, 84	2.048 ns					1, 84	0.466 ns	
V x T	2, 84	0.497 ns		2, 84	0.598 ns			Homogeneity of variance violated, analyzed by site		2, 84	1.664 ns	
V x Y	2, 84	**4.870****		2, 84	**5.596****					2, 84	**3.491***	
T x Y	1, 84	1.837 ns		1, 84	3.465 ns					1, 84	0.328 ns	
V x T x Y	2, 84	1.569 ns		2, 84	0.823 ns					2, 84	1.126 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 2.3 Results of 2-way analysis of variance on biomass components of deciduous and evergreen shrubs that were analyzed from only one vegetation type. Post-hoc tests indicate the direction of significant differences:'11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Total biomass			Old stems			New Stems			Leaves		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Ledum palustre								(rank)				
Treatment	1, 28	1.534 ns		1, 28	2.652 ns		1, 28	**5.691***	**S<C**	1, 28	2.399 ns	
Year	1, 28	**36.447*** **	**'11<'10**	1, 28	**39.669*** **	**'11<'10**	1, 28	1.641 ns		1, 28	1.030 ns	
Treatment x Year	1, 28	2.393 ns		1, 28	3.072 ns		1, 28	**7.262***		1, 28	0.216 ns	
Vaccinium uliginosum												
Treatment	1, 28	0.011 ns		1, 28	0.012 ns		1, 28	0.011 ns		1, 28	0.714 ns	
Year	1, 28	**7.845****	**'11>'10**	1, 28	**7.219***	**'11>'10**	1, 28	3.291 ns		1, 28	**5.292***	**'11>'10**
Treatment x Year	1, 28	1.100 ns		1, 28	0.415 ns		1, 28	0.085 ns		1, 28	**4.556***	
Vaccinium vitis-idaea											(rank)	
Treatment	1, 28	0.572 ns		1, 28	0.064 ns		1, 28	0.01 ns		1, 28	2.053 ns	
Year	1, 28	**10.772****	**'11>'10**	1, 28	**14.048*** **	**'11>'10**	1, 28	**10.926****	**'11>'10**	1, 28	**36.089*** **	**'11>'10**
Treatment x Year	1, 28	1.479 ns		1, 28	0.002 ns		1, 28	0.071 ns		1, 28	0.148 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 2.4 Results of 3-way analysis of variance on plant traits of graminoids that occurred in multiple vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Mass/tiller			Leaf area			Specific leaf area			# tillers		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Carex bigelowii								(log)			(rank)	
Vegetation type (V)	2, 84	1.938 ns		2, 84	1.081 ns		2, 84	**3.913***	**L, T<I**	2, 84	**5.965****	**L>I, T**
Treatment (T)	1, 84	0.158 ns		1, 84	1.508 ns		1, 84	1.503 ns		1, 84	0.601 ns	
Year (Y)	1, 84	0.956 ns		1, 84	1.006 ns		1, 84	0.656 ns		1, 84	**9.667****	**'11>'10**
V x T	2, 84	0.121 ns		2, 84	2.36 ns		2, 84	0.227 ns		2, 84	1.032 ns	
V x Y	2, 84	0.757 ns		2, 84	**3.981***		2, 84	1.788 ns		2, 84	0.723 ns	
T x Y	1, 84	0.568 ns		1, 84	0.517 ns		1, 84	0.255 ns		1, 84	0.132 ns	
V x T x Y	2, 84	0.826 ns		2, 84	0.809 ns		2, 84	0.714 ns		2, 84	0.184 ns	
Eriophorum angustifolium		(log)			(log)						(rank)	
Vegetation type (V)	2, 45	**52.274*****	**I<T**	2, 56	**43.233*****	**I<T**	2, 45	1.075 ns		2, 56	**96.586*****	**I<T**
Treatment (T)	1, 45	1.646 ns		1, 56	3.875 ns		1, 45	1.244 ns		1, 56	**37.151*****	**S>C**
Year (Y)	1, 45	3.677 ns		1, 56	**15.424*****	**'11<'10**	1, 45	3.073 ns		1, 56	**585.236*****	**'11>'10**
V x T	2, 45	1.869 ns		2, 56	**6.704***		2, 45	1.018 ns		2, 56	0.002 ns	
V x Y	2, 45	0.007 ns		2, 56	2.7979 ns		2, 45	0.136 ns		2, 56	0.002 ns	
T x Y	1, 45	**4.283***		1, 56	**4.266***		1, 45	1.530 ns		1, 56	**5.143***	
V x T x Y	2, 45	2.896 ns		2, 56	2.083 ns		2, 45	0.303 ns		2, 56	0.002 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 2.5 Results of 2-way analysis of variance on plant traits of graminoids for species that did not occur in all vegetation types. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Mass/tiller			Leaf area			Specific leaf area			# tillers		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Eriophorum vaginatum								(log)			(rank)	
Treatment	1, 28	**5.655***	**S>C**	1, 28	**11.599****	**S>C**	1, 28	1.927 ns		1, 28	3.118 ns	
Year	1, 28	0.759 ns		1, 28	0.483 ns		1, 28	3.610 ns		1, 28	0.013 ns	
Treatment x Year	1, 28	2.783 ns		1, 28	2.624 ns		1, 28	3.508 ns		1, 28	3.118 ns	
Arctagrostis latifolia												
Treatment	1, 28	0.548 ns		1, 28	0.021 ns		1, 28	Homogeneity of		1, 28	2.005 ns	
Year	1, 28	3.723 ns		1, 28	0.024 ns		1, 28	variance violated,		1, 28	**9.210****	**'11>'10**
Treatment x Year	1, 28	0.021 ns		1, 28	2.634 ns		1, 28	analyzed by year		1, 28	2.005 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 2.6 Results of 3-way analysis of variance on plant traits of deciduous shrubs that occurred in all vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	# of branches			Secondary growth rate			# of leaves			Leaf area			Specific leaf area		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
*Betula nana**		(rank)			(rank)			(rank)			(rank)				
Vegetation type (V)	2, 84	**18.944*** **	**L<I, T**	2, 84	**98.657*** **	**L<I<T**	2, 84	**10.561*** **	**L<I, T**	2, 84	**23.956*** **	**L<I<T**			
Treatment (T)	1, 84	0.614 ns		1, 84	**9.877** **	**S<C**	1, 84	0.435 ns		1, 84	0.311 ns				
Year (Y)	1, 84	**16.021*** **	**'11>'10**	1, 84	**18.168*** **	**'11<'10**	1, 84	**22.064*** **	**'11>'10**	1, 84	**21.601*** **	**'11>'10**	Homogeneity of variance violated, analyzed by site		
V x T	2, 84	0.588 ns		2, 84	**3.406***		2, 84	0.422 ns		2, 84	1.045 ns				
V x Y	2, 84	1.113 ns		2, 84	2.117 ns		2, 84	0.550 ns		2, 84	0.810 ns				
T x Y	1, 84	2.049 ns		1, 84	0.511 ns		1, 84	2.059 ns		1, 84	3.241 ns				
V x T x Y	2, 84	1.556 ns		2, 84	0.498 ns		2, 84	**4.468***		2, 84	**4.304***				
Salix pulchra		(rank)			(rank)			(log)			(log)				
Vegetation type (V)	2, 84	**39.183*** **	**L<I, T**	2, 84	**37.921*** **	**L<I, T**	2, 84	**39.018*** **	**L<I<T**	2, 84	**40.396 *** **	**L<I, T**	2, 84	**9.532*** **	**L,I<T**
Treatment (T)	1, 84	**11.986*** **	**S<C**	1, 84	**4.270***	**S>C**	1, 84	**14.316*** **	**S>C**	1, 84	**15.628*** **	**S>C**	1, 84	0.260 ns	
Year (Y)	1, 84	3.422 ns		1, 84	**9.742** **	**'11>'10**	1, 84	3.671 ns		1, 84	0.344 ns		1, 84	0.911 ns	
V x T	2, 84	1.638 ns		2, 84	**10.814*** **		2, 84	**3.177***		2, 84	1.170 ns		2, 84	2.227 ns	
V x Y	2, 84	2.520 ns		2, 84	0.927 ns		2, 84	**4.319***		2, 84	**3.304***		2, 84	0.779 ns	
T x Y	1, 84	0.904 ns		1, 84	0.109 ns		1, 84	1.045 ns		1, 84	1.251 ns		1, 84	0.222 ns	
V x T x Y	2, 84	0.984 ns		2, 84	0.195 ns		2, 84	0.575 ns		2, 84	0.54 ns		2, 84	0.526 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 2.7 Results of 2-way analysis of variance on plant traits of deciduous and evergreen shrubs that were analyzed from only one vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	# of branches			Secondary growth rate			# of leaves			Leaf area			Specific leaf area		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Ledum palustre															
Treatment	1, 28	Homogeneity of		1, 28	**92.694*** **	**S<C**	1, 28	**4.809***	**S<C**	1, 28	2.674 ns		1, 28	2.674 ns	
Year	1, 28	variance violated,		1, 28	0.612 ns		1, 28	0.034 ns		1, 28	3.106 ns		1, 28	3.106 ns	
Treatment x Year	1, 28	analyzed by year		1, 28	**12.407** **		1, 28	0.185 ns		1, 28	0.016 ns		1, 28	0.016 ns	
Vaccinium uliginosum					(rank)										
Treatment	1, 28	1.450 ns		1, 28	**19.463*** **	**S<C**	1, 28	0.249 ns		1, 28	0.297 ns		1, 28	0.351 ns	
Year	1, 28	**14.172*** **		1, 28	3.966 ns		1, 28	1.955 ns		1, 28	**4.878***	**'11>'10**	1, 28	0.042 ns	
Treatment x Year	1, 28	1.002 ns		1, 28	0.546 ns		1, 28	0.278 ns		1, 28	0.857 ns		1, 28	0.533 ns	
Vaccinium vitis-idaea					(rank)										
Treatment	1, 28	1.309 ns		1, 28	**103.06*** **	**S>C**	1, 28	0.029 ns		1, 28	0.129 ns		1, 28	3.990 ns	
Year	1, 28	**9.906** **		1, 28	**5.009***	**'11<'10**	1, 28	4.161 ns		1, 28	**5.398***	**'11>'10**	1, 28	**6.042***	'11>'10
Treatment x Year	1, 28	4.011 ns		1, 28	3.380 ns		1, 28	2.596 ns		1, 28	1.844 ns		1, 28	3.035 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

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Chapter 3

EFFECTS OF INCREASED SNOW ON NUTRIENT CONTENT OF ARCTIC PLANTS[1]

ABSTRACT

Shrub expansion in the Arctic may be enhanced by deep snow conditions, because snow insulates the soil below resulting in warmer soil temperatures and potentially increased nutrient availability for plants at spring thaw. We used three snow fences located across a gradient of shrub height and density at Toolik Field Station to compare plant nutrient uptake and carbon (C) and nitrogen (N) partitioning among plant tissues on either side of the fences. Overall, few species responded by changing their aboveground nutrient allocation patterns in response to increased snow; instead, pool size responses appeared to be driven by patterns in growth. The deciduous shrub *Salix pulchra* however, showed increased C:N content in stems, indicating increased C allocation to woody tissues. This supports previous findings of increased secondary growth in this species, which enabled further branching and leaf production. These results indicate that C accumulation in stems may play a large part in the expansion of deciduous shrubs across the Arctic and may influence ecosystem nutrient cycling and C storage.

INTRODUCTION

Both increased snowfall in the Arctic, predicted under some climate change scenarios (Maxwell 1992), and deeper snow conditions due to drift formation around expanding shrub patches (Sturm et al. 2001a) may result in ecosystem-wide changes in plant community structure and composition. Some of the major projected effects of increased snow depth in the Arctic are increased winter soil temperatures due the

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insulating effects of snow (Schimel et al. 2004, Sturm et al. 2005) and shortened growing seasons due to later melt-out of deeper drifts (Wipf and Rixen 2010). Both of these potential features of increased snow could alter plant growth significantly, as warmer soil temperatures could mean increased nutrient availability for plants at spring thaw (Sturm et al. 2001a, Schimel et al. 2004, Natali et al. 2011) and a shorter growing season could affect the timing and amount of growth by plants (Borner et al. 2008, Cooper et al. 2011). It has been hypothesized that shrub expansion in the Arctic may be perpetuated by deeper snow, because shrubs can better trap blowing snow across the tundra and subsequently benefit from increased nutrient availability which they can direct toward increased growth (Jones et al. 2001, Sturm et al. 2001a, 2001b, Walker et al. 2001).

Previous snow fence studies have documented numerous changes in arctic plant community structure in response to increased snow. Notably, species composition shifts to favor deciduous shrubs and graminoids and decreases in species diversity have been seen as other species are outcompeted (Seastedt and Vaccaro 2001, Wahren et al. 2005). This indicates that deeper snow affects species very differently, allowing some to thrive and causing others to decrease in abundance. As species composition changes, so too will ecosystem nutrient regimes, as different plant species use nutrients differently for growth. Nutrient concentration in plant tissues influences litter quality and therefore decomposition rates, and ultimately the rates of ecosystem nutrient cycling (Cornelissen 1996, Hobbie and Gough 2002, Aerts 2006, Buckeridge et al. 2009). Thus the effects of increased snow in the Arctic will likely be driven by how plants use nutrients for growth.

A plant's resource allocation strategy, where it chooses to invest acquired nutrients, has direct implications for productivity and growth, tissue nutrient concentration and nutrient storage. Thus plant allocation strategy plays an integral role in determining a plant's ability to sequester and utilize resources (Grime 1977, Komarkova and McKendrick 1988), which in turn allows them to respond to changing environmental conditions, such as those predicted by global climate change (Lambers et al. 2008). Deeper snow conditions may influence plant nutrient uptake, which will likely have

different effects for different plants because growth strategies, nutrient requirements, and nutrient allocation patterns differ considerably among plant species and functional types. Arctic plant communities include many plant functional types, but we chose to focus on the three most common ones for this study: deciduous shrubs, evergreen shrubs and graminoids (Chapin et al. 1995b). In order to predict how these different functional types will change nutrient use in response to increased snow, it is necessary to understand their growth and nutrient accumulation habits. In general, evergreen plants are slow-growing, and experience low tissue turnover and production, whereas deciduous shrubs and graminoids are fast-growing and often experience quick tissue turnover and production (Shaver and Kummerow 1992, Diaz and Cabido 1997). Because deciduous species and graminoids grow quickly, they often respond most rapidly to increased nutrient availability by increasing their growth rate. In contrast, the inherently slow growth of evergreen species may limit their capacity to translate increased nutrient uptake into growth, resulting in excess nutrients stored for future use. As a result, it is reasonable to expect tissues of evergreen species to accumulate nutrients for use during times of nutrient stress (Chapin 1980), whereas the tissues of deciduous species may not change in nutrient concentration because they may instead distribute nutrients among new plant tissues.

Allocation of resources within a plant may also, in part, be determined by habitat nutrient status. Even though plant growth in arctic ecosystems is often N-limited, the tundra can range in productivity from tussock tundra containing a variety of small-statured plants, to riparian tundra, dominated by large deciduous shrubs. Nutrient allocation strategies may vary even within species among these habitat types, and species growing in more productive areas tend to be more plastic in their allocation patterns and therefore more responsive to environmental change (McGraw and Fetcher 1992). This implies that growth responses to increased nutrient availability may be habitat dependent, with the strongest responses seen in more productive areas where plants are inherently larger and can more efficiently utilize nutrients to increase growth.

The goal of this study was to determine how plant species of different plant functional types change nutrient partitioning in response to increased snow, and how these changes may vary across tundra habitat types. We predict that growth responses will drive nutrient responses and hypothesize that 1) deciduous shrubs and graminoids will show increases in nutrient pool size as plants get bigger in response to increased snow, but will show no change in tissue nutrient concentrations because plants will distribute increased nutrient uptake among new tissues instead of accumulating nutrients in existing tissues. We also hypothesize that 2) evergreen shrubs will increase nutrient pools sizes by increasing tissue nutrient concentrations, because they will exhibit smaller growth responses in response to increased snow and rather accumulate nutrients in current tissues. Further, we hypothesize that 3) these plant responses to increased snow will be greater as shrub height and density increase along a natural productivity gradient from tussock tundra to shrub tundra. By determining how individual plants change nutrient allocation strategies in response to deeper snow, we hope to better predict how ecosystem-level nutrient cycling and associated processes may be altered under continued climate change.

METHODS

Site description

This study was conducted near the Toolik Field Station (68.38°N 149.36°W), site of the Arctic Long Term Ecological Research (LTER) project located in the foothills of the North Slope of the Brooks Range, Alaska. Mean annual air temperature is approximately -10°C and mean annual precipitation is 318 mm, of which 43% falls as snow. Average ambient snow depth is 50 cm, though snow distribution is variable due to drifting from wind (DeMarco et al. 2011). In order to address our hypotheses we collected plant samples at experimental snow fences near Toolik Field Station.

A detailed description of the experimental snow fences is provided by Addis et al. (ch. 2) and DeMarco et al. (2011). Briefly, four snow fences were constructed in 2005 near

Toolik Lake in three different vegetation types: (1) low shrub (tussock tundra with a canopy height of approx. 6 cm), (2) intermediate shrub (shrub tundra with a canopy height of approx. 32 cm), and (3) tall shrub (shrub tundra with a canopy height of approx. 55 cm) (Bret-Harte, unpublished data, DeMarco et al. 2011). One fence was erected in each site except at the tall shrub tundra site where two shorter fences were used due to patchy distribution of tall shrubs. Fences are 1.5 m tall and 60 m long, except at the tall shrub site where there are two 30-m fences. Fences run east-west and snow drifts of greater than one m in depth accumulate on the north sides of the fences (Bret-Harte, unpublished data, Addis, unpublished data).

Ramet and tiller harvest

Eight ramets (large, rooted branches) of each deciduous and evergreen shrub species were haphazardly collected from each side of the snow fence at each site during the first two weeks of August in 2010 and 2011. Haphazard collection involved walking a transect the length of the fence and stopping roughly every 10 steps to collect the nearest individual that appeared to be at least eight or nine years of age. In total 16 samples of each species were collected from each snow fence each year, eight from each side of the fence. Ramets were collected from along the entire length of each snow fence, taking care to collect within 2-10 m from the snow fence on the drift side to ensure that plants were covered by winter snow drifts. On the control side, plants were collected at least 10 m from the fence to ensure that they were in a zone of ambient snow depth. For graminoids species, eight mother-daughter tiller complexes were haphazardly collected in the same manner as described above. A mother-daughter tiller complex is defined as an individual tiller (mother) with at least 1 immature tiller (daughter) growing from the same rhizome. For tussock forming species, such as *Eriophorum vaginatum*, a wedge of the tussock was removed to ensure collection of at least one mother-daughter tiller complex. All ramets and tiller complexes were transported to the laboratory for carbon (C) and nitrogen (N) analysis. Nomenclature for species follows Hultén (1968).

Carbon and nitrogen analysis

Samples were prepared for C and N content analysis in the laboratory by separating woody ramets into three parts: leaves, new stems (formed in the current year) and old stems. For woody species, only the most apical 8-9 years of stem growth were analyzed. For graminoids, we analyzed only green blades for nutrient content; all other plant parts were discarded. All plant material was dried at 60 degrees C for at least 48 hours and then ground into a fine powder using a ball mill or high-energy ball mill for especially coarse material, such as large stems. Samples were analyzed for C and N content by weight using a LECO TruSpec CN Carbon/Nitrogen Analyzer (LECO Corporation, St. Joseph, Michigan. When there was not enough plant material to meet instrument requirements (100 mg), such as in the case of stems, new and old stems were combined to produce enough material. If there was not enough total stem material, or enough of other plant tissue types, the analysis was not run. For all woody species sampled at the low shrub vegetation type, new stems were combined with old stems for analysis as well as new and old stems of *V. uliginosum* at the intermediate shrub vegetation type. For *V. vitis-idaea,* only leaves were analyzed, due to overall low wood production. For graminoids species, mother and daughter tillers were ground and analyzed separately.

Calculation of carbon and nitrogen pools, CN ratio

Carbon and N pools were calculated by multiplying the average C or N content (%) by the biomass of that plant part for each species (Addis et al. (ch 2). Since some individual samples could not be analyzed for C and N due to insufficient material, we used the average C and N content for each species, at each vegetation type, for each treatment, in each year, which we multiplied by plant biomass so that species for which we had biomass data, but no nutrient data, could be included in the dataset. For graminoids, average C and N pools were calculated using both mother and daughter tillers, since preliminary analysis by ANOVA showed mother and daughter tiller nutrient content was not significantly different. C:N ratios were determined from nutrient

concentrations for only those samples actually analyzed for C and N; no averages were used in this calculation, thus small samples were excluded.

Statistical analysis

We used a combination of one, two and three-way analyses of variance (ANOVAs) to analyze for treatment effects for each species at each snow fence location. Vegetation type (low shrub, intermediate and tall shrub) was included as a random effect, with snow fence treatment as the fixed effect. Because sampling occurred over two years, year was included as a blocking factor. For species occurring at more than one snow fence location, an initial three-way ANOVA was run for each growth variable (General linear model (GLM) with vegetation type, treatment, and year as main effects and all possible interactions between the three factors). For species occurring at only one snow fence, an initial two-way ANOVA was run for each growth variable (GLM with treatment and year as main effects and a treatment x year interaction). If statistically significant treatment effects for any growth variable, or a significant interaction involving treatment were found, subsequent two-way (for species occurring at multiple site) and one-way (for species occurring only at one site and having a significant treatment x year interaction) ANOVAs were run to determine for which sites and years the treatment effect was significant. In this paper, we present only tables including initial results from the two or three-way ANOVAs (depending on how many sites the species were samples from); tables containing results from two and one-way ANOVAs resulting from subsequent analyses are provided in Appendix B.

All data were transformed prior to analysis by ANOVA if necessary to achieve normality and homoscedasticity of variance. If these assumptions were not met, data were either logarithmically or rank-transformed and ANOVAs were run on the transformed data (Zar 1999). If analyses on transformed data produced a significant interaction effect, we ran individual 2-way ANOVAs because of the difficulty of interpreting interactions of rank-transformed data due to its nonlinear nature (Quinn and Keough 2002). Still, in some cases, model assumptions could not be met by transforming the data. In these cases, data were separated first by site, then by year, transformed if

needed, and analyzed separately. In these instances, we were unable to test for interaction effects between factors. All statistical analyses were performed in JMP 4.0.2 and an alpha level of 0.05 was considered statistically significant.

RESULTS

Nitrogen pools

For woody species, the total N pool per ramet increased with snow addition for only one of five species sampled, *Salix pulchra* (Table 3.1, Fig. 3.1). When analyzed by site, this increase was strongest at the intermediate site ($F_{1,28}$=8.404, p<0.01), but because of a significant interaction between sampling year and treatment ($F_{1,28}$=5.33, p<.05), we looked at years separately and found that snow enhanced the total N pool 2-fold relative to control plants in 2011 ($F_{1,14}$=7.894, p<0.05) and had no effect in 2010 ($F_{1,14}$=0.639, p>0.05). Breaking apart the total N pool per ramet into its contributing parts, *S. pulchra* N pools increased significantly under snow addition in new stems and leaves, but not old stems (Table 3.1, Fig. 3.1). Across sites, new stem N pools could not be transformed to meet model assumptions of homogeneity of variance, so sites were analyzed separately. We found the new stem N pool was enhanced 1.8-fold by snow at the intermediate site ($F_{1,28}$=5.554, p<0.05), but was unaffected at the tall site ($F_{1,28}$=2.221, p>0.05) (Fig. 3.1). Leaf N pools were also enhanced by snow (Table 3.1, Fig. 3.1); broken down by site, this roughly 2-fold increase was only apparent at the intermediate and tall sites (intermediate: $F_{1,28}$=9.313, p<0.01, tall: $F_{1,28}$=7.695, p<0.01).

None of the other woody species (*B. nana, V. uliginosum, L. palustre, V. vitis-idaea)* showed increases in either total N pools or leaf N pools with added snow (Tables 3.1, 3.2, Fig. 3.1). Only *L. palustre* (in addition to *S. pulchra*) showed increased stem N pools under snow addition (1.8-fold); all other species also showed no difference in stem N pools, either new or old, with added snow (Tables 3.1, 3.2, Fig. 3.1). For graminoid species, tiller N pools increased with snow addition in two of the four graminoids sampled (Tables 3.3, 3.4, Fig. 3.2). Tiller N pools of *Eriophorum vaginatum* increased

1.8- fold under snow addition, and tiller N pools of *E. angustifolium* also increased, but only at the intermediate site ($F_{1, 25}$=20.5236, p<0.0001). *Carex bigelowii* and *A. latifolia* did not change tiller N pools under snow addition (Tables 3.3, 3.4, Fig. 3.2).

Across species occurring at multiple sites, N pools generally increased from low shrub to tall shrub sites, except for *C. bigelowii*, where there was no effect of vegetation type on tiller N pools (Tables 3.1, 3.2, 3.3, 3.4, Figs. 3.1, 3.2).

Carbon pools

For woody species, only *S. pulchra* showed any changes in C pools in response to snow addition; all other woody species showed no changes (Tables 3.5, 3.6, Fig. 3.3). Results in this section, therefore, refer only to *S. pulchra.* The total C pool increased with snow addition, and further analysis by site indicated that this increase was strongest at the intermediate site ($F_{1,28}$=12.581, p<0.01), but because of a significant interaction between sampling year and treatment ($F_{1,28}$=7.565, p<.05), we looked at years separately and found that snow enhanced total C pools 2.7-fold relative to control plants in 2011 ($F_{1,14}$=11.747, p<0.01) and had no effect in 2010 ($F_{1,14}$=0.602, p>0.05). Looking at plant components separately, *S. pulchra* C pools increased significantly under snow addition in new stems, old stems, and leaves (Table 3.5, Fig. 3.3). Across sites, new stem C pools could not be transformed to meet model assumptions of homogeneity of variance, so sites were analyzed separately. We found new stem C pools were enhanced 2-fold by snow at the intermediate site ($F_{1,28}$=7.481, p<0.05), but were unaffected at the tall site ($F_{1,28}$=2.024, p>0.05) (Fig. 3.3). Old stem C pools were also enhanced by snow addition, and further analyses revealed this response was driven by a 3-fold increase at the intermediate site ($F_{1,28}$=12.646, p<0.01) in 2011 ($F_{1,14}$=13.237, p<0.01). Similar to leaf N pools, leaf C pools were also enhanced by snow (Table 3.5, Fig. 3.3); broken down by site, this roughly 2-fold increase was only apparent at the intermediate and tall sites (intermediate: $F_{1,28}$=10.191, p<0.01, tall: $F_{1,28}$=8.078, p<0.01).

For graminoid species, tiller C pools increased with snow addition in two of the four graminoids sampled, as seen with the N pools (Tables 3.3,3. 4, Fig. 3.4). Tiller C pools of *Eriophorum vaginatum* increased 1.7- fold under snow addition, and tiller C

pools of *E. angustifolium* also increased, driven by a 1.5- fold increase at the intermediate site ($F_{1, 25}$=17.573, p<0.0001). *Carex bigelowii* and *A. latifolia* did not change Tiller C pools under snow addition (Tables 3.3, 3.4, Fig. 3.4).

Across species occurring at multiple sites, C pools generally increased from low shrub to tall shrub sites, except for *C. bigelowii*, where C pools were larger at the low site than at the intermediate site, with the tall site falling in between (Tables 3.3, 3.5, 3.6, Figs. 3.3, 3.4). In some cases, C pools were not statistically different between intermediate and tall sites (*S. pulchra*), though an increasing trend was seen from the intermediate to the tall site (Table 3.5, Fig. 3.3).

C:N

Most species' C:N ratios in stems and leaves did not change with added snow; only two species, *S. pulchra* and *L. palustre*, altered their C:N ratios in response to snow (Tables 3.3, 3.4, 3.7, 3.8. Fig. 3.5). Of all the plant components analyzed (old stems, new stems, leaves), only old stems of *S. pulchra* increased their C:N ratio under snow addition (Table 3.7, Fig. 3.5) and further analysis revealed this response was driven by roughly 1.2-fold increases at both the low and intermediate sites (low: $F_{1,27}$=6.126, p<0.05, intermediate: $F_{1, 28}$=15.723, p<0.001). *Ledum palustre*, on the other hand, showed a decreased C:N ratio in stems with added snow, which was driven mainly by the 5% decrease in stem C:N seen in 2010 ($F_{1, 9}$=12.796, p<0.01).

Across species occurring at multiple sites, C:N ratios generally showed no effect of vegetation type, except for *S. pulchra*, which showed somewhat opposite patterns in old stems and leaves (Tables 3.3, 3.4, 3.7, 3.8, Fig. 3.5). Old stems from the low and intermediate sites had higher C:N ratios than those from the tall site, whereas leaves from the low site had lower C:N ratios than those from the intermediate or tall site (Table 3.7, Fig. 3.5).

DISCUSSION

Nutrient pools sizes are driven by growth

Overall, very few species responded by changing their aboveground nutrient allocation patterns in response to increased snow; instead, pool size responses appeared to be driven by patterns in growth. Plant responses to increased snow fell into three categories: those that changed nutrient allocation in certain tissues, those that showed increases in both C and N pool sizes, and those that showed no change in nutrient allocation in response to snow.

In several species, both C and N pools of both stems and leaves increased with added snow, indicating the plants simply got bigger, increasing total size but not relative allocation of C or N in aboveground tissue (Addis et al. (ch 2)). In this category are leaves of *E. angustifolium* and *E. vaginatum*, and the new stems and leaves of *S. pulchra*. Nutrient pools in plant tissues have shown increases in response to fertilization in the Arctic (Chapin et al. 1995a, Chapin and Shaver 1996), thus it seems likely that nutrient availability was increased under snow addition and these plants were able to use the extra nutrients for overall growth, but did not change nutrient partitioning in aboveground tissue. This partially supports our hypothesis that deciduous shrubs, with the exception of *B. nana*, and some graminoids increased nutrient pools by increasing biomass, even though nutrient allocation remained unchanged. Indeed, previous research has shown that leaf C:N ratios of some deciduous shrubs do not change under added snow (Welker et al. 2005).

In addition, increases in nutrient pools in both *S. pulchra* and *E. angustifolium* were highest at the intermediate site, which provides some support for our hypothesis that responses would be greater along a gradient of site productivity, though responses generally didn't increase at the tall site. This maximum response of shrubs of intermediate size was also seen in plant biomass, and we postulate that plants at the tall sites may not have been as nutrient-limited due to different environmental factors, and therefore increasing nutrient availability had marginal effects.

Several species (*B. nana, V. uliginosum, V. vitis-idaea, C. bigelowii,* and *A. latifolia*), however, showed no change in C or N pools in response to snow addition; these species similarly showed no change in biomass (Addis et al. (ch 2)). One possible reason for this may be that other factors may be limiting for these species besides nutrient availability. Excluding *B. nana*, all of these species are often found in the understory where they may be subject to light limitation which may result in decreased nutrient uptake and growth (Chapin et al. 1995a). As discussed in chapter 2, it's possible that nutrient uptake and growth of *B. nana* may be suppressed under added snow due to increased pathogen activity (Sturges 1989). Another factor preventing increased tissue nutrient content could be that these species were simply outcompeted by other species, and were not able effectively capture and use available nutrients.

Two species changed nutrient allocation

Two species, *S. pulchra* and *L. palustre*, showed changes in C or N partitioning to specific plant parts, rather than making more or less of a particular tissue with fixed nutrient concentrations, as described above. The C:N ratio of old stems was significantly increased for *S. pulchra* and decreased for *L. palustre* under snow addition. While both C and N pools of old stems increased significantly, it seems that *S. pulchra* at the intermediate snow-fence site was increasing the proportional partitioning of C to old stems per unit N. Forest ecosystems have also shown respiration rates of wood (closely linked to N content) did not increase under increased nutrient availability, even though C allocation to woody tissues increased (Ryan et al. 1996), likely because the low maintenance cost of woody tissues may not increase proportionally with biomass. Though unpredicted, this change in allocation substantiates increases documented in stem biomass and secondary growth of *S. pulchra* under snow addition (Addis et al. (ch 2)). Since C is readily available for canopy plants in the high light conditions of the arctic summer, increasing allocation to C-rich stems is an economical way for a plant to increase biomass, especially as it provides increased structural support for further branching and leaf production (Addis et al. (ch 2)). Indeed, cellulose and hemicellulose, major components of the structural material in plants, are relatively "cheap" to produce in

terms of the cost of synthesis per unit N (Chapin 1989). Forest trees have also shown significant increases in carbon partitioning to wood under increasing nutrient availability, while partitioning to leaves remained constant, similar to our findings (Litton et al. 2007). Increased carbon partitioning in stems, along with documented increases in stem biomass and secondary growth (chapter 2), provide compelling evidence that wood is sensitive to environmental change and may drive plant responses to changing nutrient regimes.

Ledum palustre, on the other hand, showed a decreased C:N ratio in stems and no change in the stem C pool under added snow, indicating *L. palustre* is increasing N partitioning to stems. As a slow-growing evergreen species, inherently less productive and less plastic than other faster-growing species, it is likely that *L. palustre* couldn't translate increased nutrient uptake into immediate growth, thereby diluting the N pool with increased biomass; instead N has accumulated in the stem tissue. This could indicate luxury consumption of N in excess of the physiological demands for growth, as has been seen with evergreen plants under increased nutrient availability (Chapin 1980). Indeed, plants from infertile sites (characteristic habitat for evergreen species) typically show less of a growth response to fertilization, but instead increase tissue nutrient concentrations (Chapin 1980). This may be because these species may have inherently slow growth rates and therefore exhibit low plasticity to changes in nutrient availability, or possibly because for understory species like *L. palustre*, carbon assimilation is more difficult due to light limitation, making it difficult for plants to synthesize C compounds needed for growth (Chapin 1989). While *L. palustre* behaved as predicted in some aspects, e.g. increasing N content in stems rather than investing in new growth, foliar N concentrations were unaffected by increased snow.

Overall, no species showed changes in nutrient allocation to leaves. Previous work has found reduced leaf C:N ratios and increases in leaf N concentration across a variety of tundra species in response to deeper snow (Walsh et al. 1997, Welker et al. 2005), so it is curious we did not see this response. We suspect this may be related to the timing of sample collection, which was done in early August. While late July/early August coincide with peak biomass, it is possible that N translocation from leaves to

stems and roots was already underway, resulting in lower leaf N concentrations than expected. It is also equally possible that added snow may delay the timing of N translocation due to delayed snowmelt and consequently delayed phenology of plants (Walsh et al. 1997). This would resulting in plants being less N depleted at this time of year compared to plants under control conditions, though further research is needed to determine how increased snow effects seasonal N depletion of plant tissues. We recognize the leaf nutrient data in this study may not be characteristic of leaf responses to changing nutrient conditions.

Implications for shrub expansion

In conclusion, these results show that tundra plant species that are able to increase C and N uptake under added snow were also able to increase biomass of the corresponding tissue. In only two cases did nutrient partitioning change, but for both cases, it was stem tissue that showed altered C or N partitioning. This suggests that allocation to wood in arctic plants may be particularly responsive to environmental change. This can result in C accumulation in deciduous shrubs, which may enable increased secondary growth, facilitating overall plant growth, or N accumulation in evergreen shrubs, likely to be stored for future use. These results indicate that C accumulation in stems may play a large part in the expansion of deciduous shrubs across the Arctic. At the broader scale, changes in nutrient partitioning in response to increased snow may influence ecosystem nutrient cycling and storage. If some plants are able to increase C storage in stems, ecosystem balance between C storage and loss may change, potentially influencing whether tundra ecosystems are carbon sources or sinks.

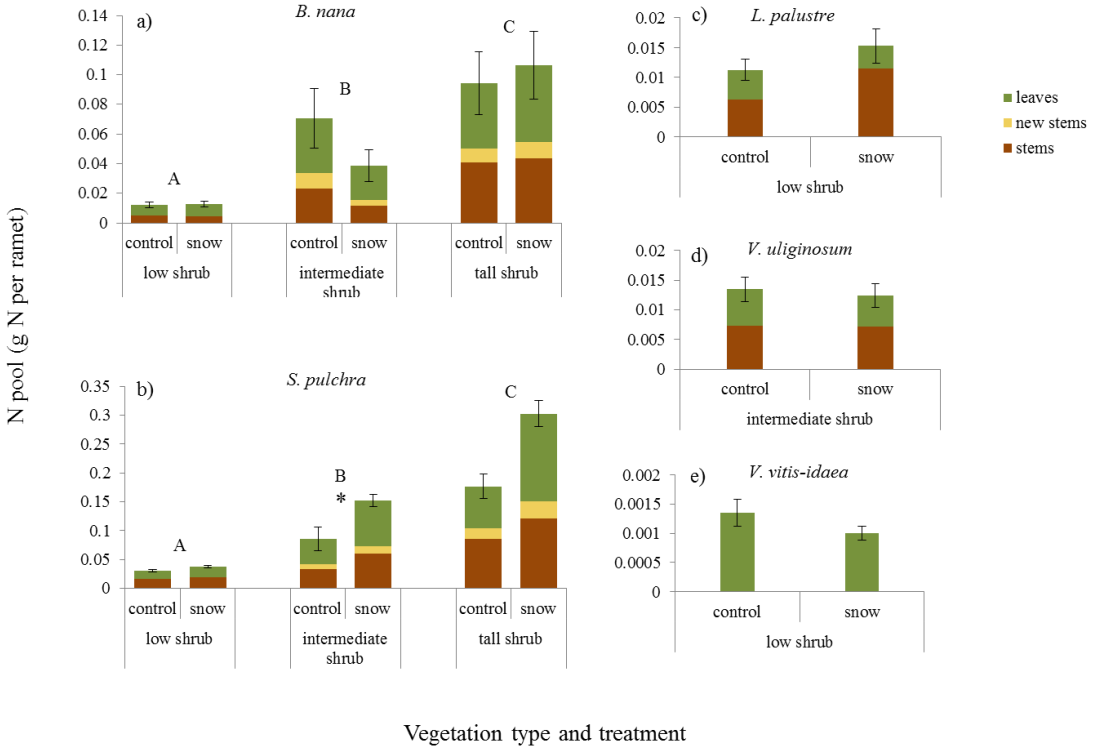

Figure 3.1 Nitrogen pools of deciduous shrubs (a, b, d) and evergreen shrubs (c, e). Total biomass is represented by the sum of old stem pools (black), new stem pools (striped), and leaf pools (gray). Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error (n=16) of the total N pool per ramet.

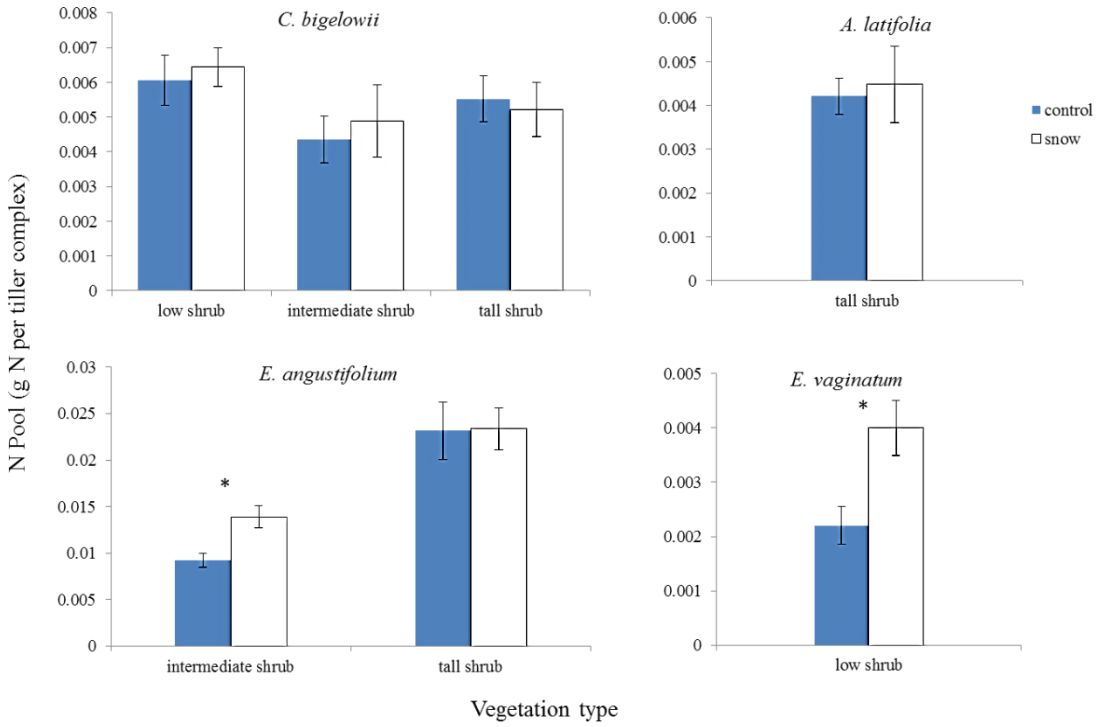

Figure 3.2 Nitrogen pools of graminoids. Statistically significant effects of snow treatment are indicated by an asterisk (*). Data were averaged over two years. Error bars represent ±1 standard error.

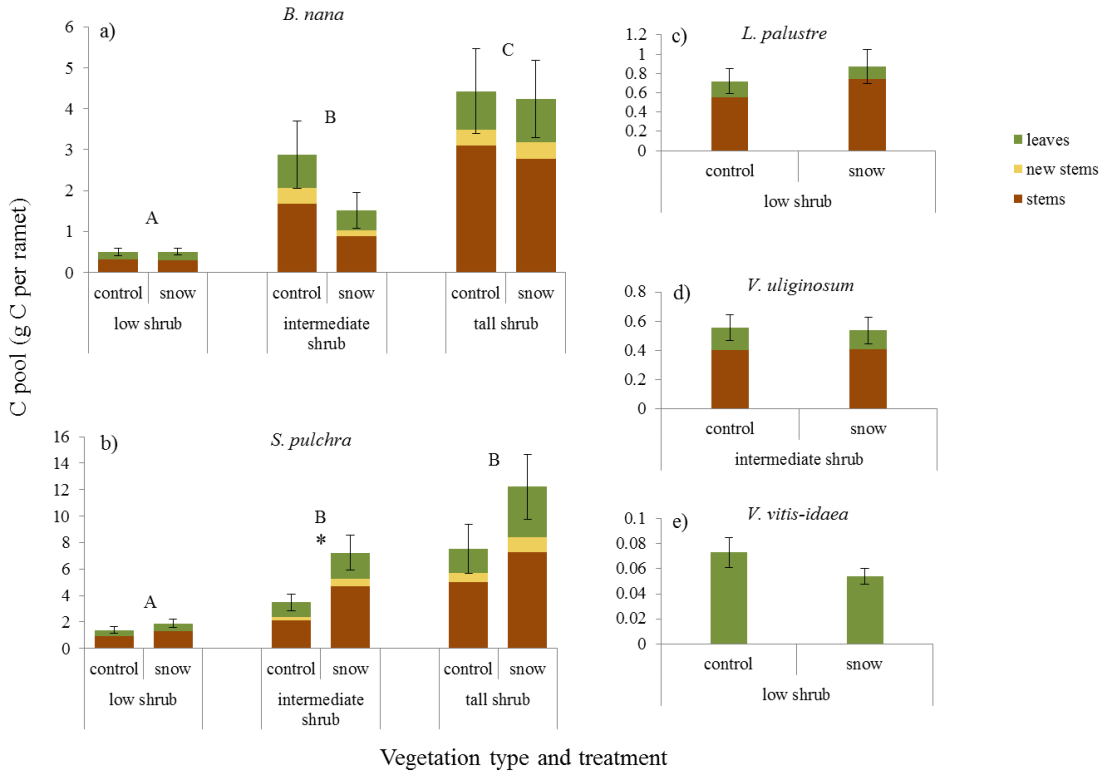

Figure 3.3 Carbon pools of deciduous shrubs (a, b, d) and evergreen shrubs (c, e). Total carbon pools are represented by the sum of old stem pools (black), new stem pools (striped), and leaf pools (gray). Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error (n=16) of the total C pool per ramet.

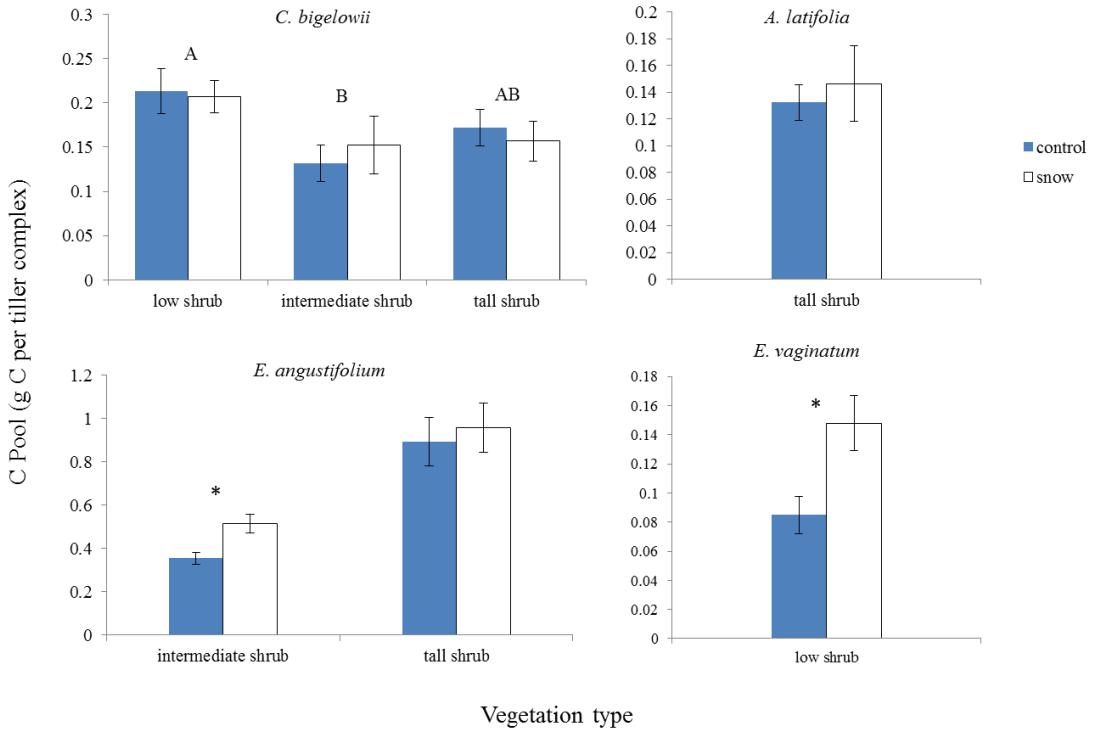

Figure 3.4 Carbon pools of graminoids. Statistically significant effects of snow treatment are indicated by an asterisk (*). Data were averaged over two years. Error bars represent ±1 standard error.

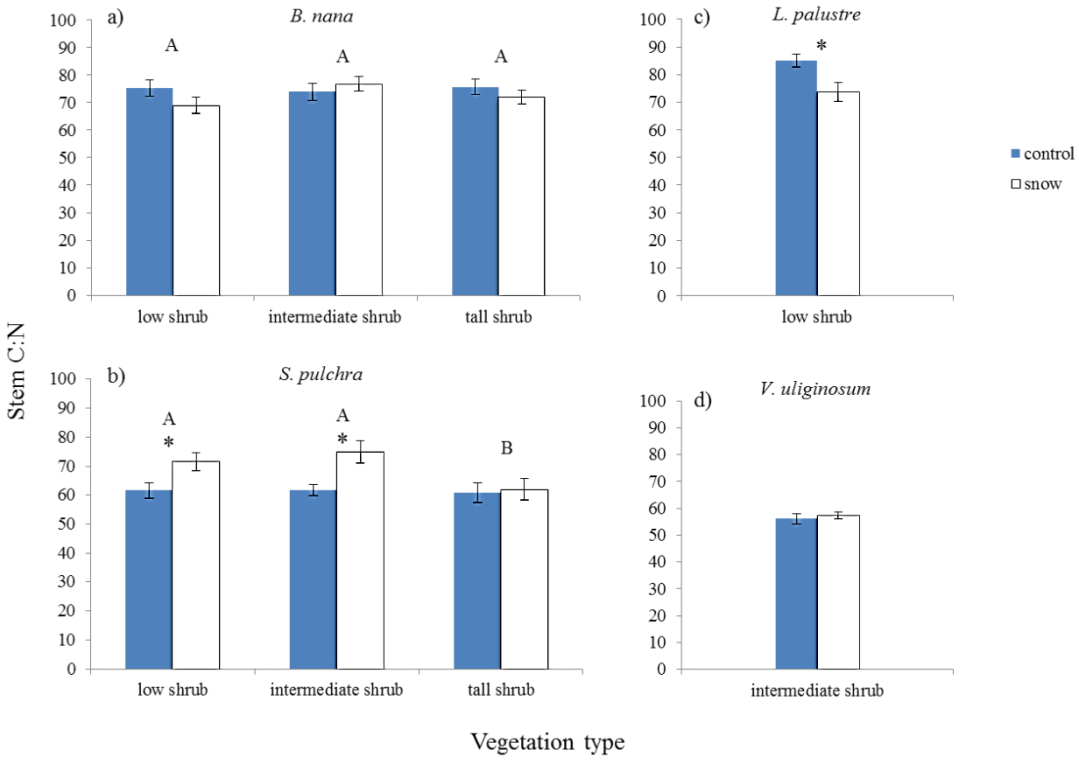

Figure 3.5 Carbon to nitrogen ratio of stems of deciduous shrubs (a, b, d) and an evergreen shrubs (c) . Statistically significant effects of snow treatment are indicated by an asterisk (*). Different letters denote significant differences between vegetation types. Data were averaged over two years. Error bars represent ±1 standard error (n=16).

Table 3.1 Results of 3-way analysis of variance on nitrogen pools of deciduous shrubs that occurred in multiple vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Total N pool			Old stem N pool			New stem N pool			Leaf N pool		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Betula nana		(rank)			(rank)						(rank)	
Vegetation type (V)	2, 84	**37.079*** **	**L<I<T**	2, 84	**32.351*** **	**L<I<T**	2, 54	1.717 ns		2, 84	**33.177*** **	**L<I<T**
Treatment (T)	1, 84	0.008 ns		1, 84	0.089 ns		1, 54	0.975 ns		1, 84	0.16 ns	
Year (Y)	1, 84	**23.403*** **	**'11>'10**	1, 84	**25.733*** **	**'11>'10**	1, 54	**9.674****	**'11>'10**	1, 84	**23.204*** **	**'11>'10**
V x T	2, 84	0.754 ns		2, 84	1.37 ns		2, 54	1.916 ns		2, 84	0.462 ns	
V x Y	2, 84	1.195 ns		2, 84	2.152 ns		2, 54	0.012 ns		2, 84	1.49 ns	
T x Y	1, 84	3.008 ns		1, 84	2.576 ns		1, 54	1.193 ns		1, 84	3.12 ns	
V x T x Y	2, 84	2.339 ns		2, 84	1.589 ns		2, 54	1.533 ns		2, 84	2.949 ns	
Salix pulchra		(rank)									(rank)	
Vegetation type (V)	2, 84	**42.393*** **	**L<I<T**	2, 84	**23.144*** **	**L<I,T**				2, 84	**63.231*** **	**L<I<T**
Treatment (T)	1, 84	**10.88*** **	**S>C**	1, 84	3.431 ns					1, 84	**16.469*** **	**S>C**
Year (Y)	1, 84	0.768 ns		1, 84	0.565 ns			Homogeneity of variance		1, 84	2.78 ns	
V x T	2, 84	0.565 ns		2, 84	0.527 ns			violated, analyzed by site		2, 84	1.336 ns	
V x Y	2, 84	**3.793***		2, 84	**4.167 ns**					2, 84	**3.179***	
T x Y	1, 84	0.805 ns		1, 84	3.431 ns					1, 84	0.099 ns	
V x T x Y	2, 84	1.410 ns		2, 84	0.849 ns					2, 84	0.882 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.2. Results of 2-way analysis of variance on nitrogen pools of deciduous and evergreen shrubs that were analyzed from only one vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Total N Pool			N pool stems			N pool leaves		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Ledum palustre					(rank)				
Treatment	1, 28	3.016 ns		1, 28	**5.046***	**S>C**	1, 28	2.103 ns	
Year	1, 28	**32.394*****		1, 28	**95.269*****	**'11<'10**	1, 28	1.884 ns	
Treatment x Year	1, 28	**4.68***		1, 28	2.646 ns		1, 28	0.191 ns	
Vaccinium uliginosum									
Treatment	1, 28	0.176 ns		1, 28	0.003 ns		1, 28	0.869 ns	
Year	1, 28	**11.471****	**'11>'10**	1, 28	**10.063****	**'11>'10**	1, 28	**7.928****	**'11>'10**
Treatment x Year	1, 28	1.683 ns		1, 28	0.29 ns		1, 28	**5.028***	
Vaccinium vitis-idaea									
Treatment	See N pool leaves			Not analyzed			1, 14	1.899 ns	
Year									
Treatment x Year									

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.3 Results of 3-way analysis of variance on nutrient pools of graminoids that occurred in multiple vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Tiller N pool			Tiller C pool			Tiller CN		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Carex bigelowii									
Vegetation type (V)	2, 72	2.132 ns		2, 72	**3.683***	**L>I**	2, 59	1.083 ns	
Treatment (T)	1, 72	0.17 ns		1, 72	0.0001 ns		1, 59	0.23 ns	
Year (Y)	1, 72	0.681 ns		1, 72	0.019 ns		1, 59	3.51 ns	
V x T	2, 72	0.218 ns		2, 72	0.31 ns		2, 59	0.553 ns	
V x Y	2, 72	1.307 ns		2, 72	0.689 ns		2, 59	2.487 ns	
T x Y	1, 72	1.011 ns		1, 72	0.486 ns		1, 59	1.002 ns	
V x T x Y	2, 72	0.48 ns		2, 72	0.419 ns		2, 59	0.068 ns	
Eriophorum angustifolium									
Vegetation type (V)	Homogeniety of variance violated, analyzed by site						1, 54	0.205 ns	
Treatment (T)							1, 54	0.131 ns	
Year (Y)							1, 54	**14.285*****	**'11<'10**
V x T							1, 54	0.197 ns	
V x Y							1, 54	0.823 ns	
T x Y							1, 54	0.444 ns	
V x T x Y							1, 54	2.368 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.4 Results of 2-way analysis of variance on nutrient pools of graminoids that were analyzed from only one vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were log-transformed where indicated.

	Tiller N pool			Tiller C pool			Tiller CN		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Arctagrostis latifolia									
Treatment	1, 28	0.073 ns		1, 28	0.194 ns		1, 24	0.325 ns	
Year	1, 28	0.191 ns		1, 28	0.009 ns		1, 24	1.011 ns	
Treatment x Year	1, 28	0.008 ns		1, 28	0.108 ns		1, 24	0.221 ns	
Eriophorum vaginatum		(ln)			(ln)				
Treatment	1, 24	**9.071****	**S>C**	1, 24	**7.205***	**S>C**	1, 11	0.888 ns	
Year	1, 24	1.557 ns		1, 24	0.739 ns		1, 11	**5.07***	
Treatment x Year	1, 24	2.619 ns		1, 24	3.778 ns		1, 11	0.118 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.5 Results of 3-way analysis of variance on carbon pools of deciduous shrubs that occurred in multiple vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank transformed where indicated in parentheses. Significant interaction effects are interpreted within the text.

	Total C pool			Old stem C pool			New stem C pool			Leaf C pool		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Betula nana		(rank)			(rank)						(rank)	
Vegetation type (V)	2, 84	**31.73*****	**L<I<T**	2, 84	**28.457****	**L<I<T**	2, 54	1.668 ns		2, 84	**28.498****	**L<I<T**
Treatment (T)	1, 84	0.152 ns		1, 84	0.375 ns		1, 54	0.949 ns		1, 84	0.016 ns	
Year (Y)	1, 84	**17.774*****	**'11>'10**	1, 84	**20.024****	**'11>'10**	1, 54	**8.189****	**'11>'10**	1, 84	**20.294****	**'11>'10**
V x T	2, 84	0.654 ns		2, 84	0.587 ns		2, 54	1.688 ns		2, 84	0.461 ns	
V x Y	2, 84	1.62 ns		2, 84	2.088 ns		2, 54	0.0001 ns		2, 84	1.454 ns	
T x Y	1, 84	3.774 ns		1, 84	2.92 ns		1, 54	0.785 ns		1, 84	**4.234***	
V x T x Y	2, 84	1.861 ns		2, 84	1.53 ns		2, 54	1.534 ns		2, 84	**3.579***	
Salix pulchra		(rank)			(rank)						(rank)	
Vegetation type (V)	2, 84	**33.143*****	**L<I,T**	2, 84	**20.973****	**L<I,T**				2, 84	**51.2*****	**L<I<T**
Treatment (T)	1, 84	**11.309*****	**S>C**	1, 84	**6.655***	**S>C**				1, 84	**17.031****	**S>C**
Year (Y)	1, 84	1.599 ns		1, 84	2.637 ns					1, 84	0.847 ns	
V x T	2, 84	0.513 ns		2, 84	0.563 ns		Homogeneity of variance violated, analyzed by site			2, 84	1.775 ns	
V x Y	2, 84	**4.748***		2, 84	**5.569****					2, 84	**3.781***	
T x Y	1, 84	1.574 ns		1, 84	3.141 ns					1, 84	0.15 ns	
V x T x Y	2, 84	1.499 ns		2, 84	0.854 ns					2, 84	1.1 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.6 Results of 2-way analysis of variance on carbon pools of deciduous and evergreen shrubs that were analyzed from only one vegetation type. Post-hoc tests indicate the direction of significant differences: '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Significant interaction effects are interpreted within the text.

	Total C pool			C pool stems			C pool leaves		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Ledum palustre									
Treatment	1, 28	0.999 ns		1, 28	2.017 ns		1, 28	2.859 ns	
Year	1, 28	**34.304*** **	**'11<'10**	1, 28	**37.965*** **	**'11<'10**	1, 28	0.856 ns	
Treatment x Year	1, 28	1.83 ns		1, 28	2.429 ns		1, 28	0.215 ns	
Vaccinium uliginosum									
Treatment	1, 28	0.026 ns		1, 28	0.0005 ns		1, 28	0.644 ns	
Year	1, 28	**9.246****	**'11>'10**	1, 28	**8.803****	**'11>'10**	1, 28	**5.305 ***	**'11>'10**
Treatment x Year	1, 28	1.137 ns		1, 28	0.453 ns		1, 28	**4.81***	
Vaccinium vitis-idaea									
Treatment	See C pool leaves			Not analyzed			1, 14	1.901 ns	
Year									
Treatment x Year									

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.7 Results of 3-way analysis of variance on CN ratios of deciduous shrubs that occurred in multiple vegetation types. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site, S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were log-transformed where indicated in parentheses.

	Old stem CN			New stem CN			Leaf CN		
Factor	df[a]	F	Post hoc	df[a]	F	Post hoc	df[a]	F	Post hoc
Betula nana									
Vegetation type (V)	2, 73	0.554 ns		1, 26	2.232 ns		2, 71	**7.151****	**L>I, T**
Treatment (T)	1, 73	1.204 ns		1, 26	0.236 ns		1, 71	1.398 ns	
Year (Y)	1, 73	0.089 ns		1, 26	**17.289****	**'11<'10**	1, 71	**6.301***	**'11<'10**
V x T	2, 73	1.30 ns		1, 26	0.447 ns		2, 71	0.124 ns	
V x Y	2, 73	**4.492***		1, 26	3.105 ns		2, 71	0.071 ns	
T x Y	1, 73	0.018 ns		1, 26	4.008 ns		1, 71	1.1 ns	
V x T x Y	2, 73	0.009 ns		1, 26	0.028 ns		2, 71	1.911 ns	
Salix pulchra								(ln)	
Vegetation type (V)	2, 83	**3.268***	**L,I>T**	2, 84			2, 81	**15.998*****	**L>I, T**
Treatment (T)	1, 83	**14.274*****	**S>C**	1, 84			1, 81	0.404 ns	
Year (Y)	1, 83	**35.14*****	**'11>'10**	1, 84	III-conditioned		1, 81	**16.249*****	**'11<'10**
V x T	2, 83	2.78 ns		2, 84	regression problem,		2, 81	0.715 ns	
V x Y	2, 83	2.38 ns		2, 84	analyzed by site		2, 81	1.017 ns	
T x Y	1, 83	3.568 ns		1, 84			1, 81	0.096 ns	
V x T x Y	2, 83	0.364 ns		2, 84			2, 81	0.545 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table 3.8 Results of 2-way analysis of variance on CN ratios of deciduous and evergreen shrubs that were analyzed from only one vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Significant interaction effects are interpreted within the text.

	CN stems			CN leaves		
Factor	df[a]	F	Post-hoc	df[a]	F	Post-hoc
Ledum palustre						
Treatment	1, 21	**9.484****	**S<C**	1, 20	2.373 ns	
Year	1, 21	0.045 ns		1, 20	**7.448***	**'11>'10**
Treatment x Year	1, 21	**7.947***		1, 20	0.045 ns	
Vaccinium uliginosum						
Treatment	1, 26	0.182 ns		1, 20	0.156 ns	
Year	1, 26	3.899 ns		1, 20	**9.37****	**'11<'10**
Treatment x Year	1, 26	0.494 ns		1, 20	0.0001 ns	
Vaccinium vitis-idaea						
Treatment	Not analyzed			1, 6	2.294 ns	
Year						
Treatment x Year						

[a] Degrees of freedom are reported as (df treatment, df error)

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Chapter 4

GENERAL CONCLUSIONS

The goal of this thesis was to understand the mechanisms underlying shrub expansion in the Arctic at the plant level; to better understand how changes in individual species' growth has led to the apparent success and expansion of some species (namely deciduous shrubs) at the expense of others. Increased shrub cover has been most commonly linked to increases in summer temperature (Blok et al. 2011, Myers-Smith et al. 2011, Frost and Epstein 2013), yet winter processes may also play an important role in shrub expansion across the Arctic (Sturm et al. 2005). We chose to study this system through the effects of increased snow on growth and allocation of arctic plants because snow is an important component of life in the Arctic, and changes in snow cover may increase nutrients available for plant update and growth (Schimel et al. 2004, DeMarco et al. 2011). We showed that increased snow does enhance growth of some species, while others were unaffected or negatively affected by added snow. We demonstrated that interactions between plants and changing resources determine which species thrive, and which may ultimately be outcompeted. Responses of individual species to environmental change are the foundation for visible landscape change, thus our work contributes crucial understanding to large-scale observations of shrub expansion in the Arctic.

We showed that increased snow most strongly benefited growth of one deciduous shrub, *Salix pulchra,* and established that increased secondary growth is the primary mechanism by which this species rapidly grows and outcompetes other species. *Salix pulchra* allocated more C to stems per unit N under snow addition, resulting in thicker, stronger stems that support increased branching and leaf production. This species is fast-growing and is typically large in size, depending on its environment, and can thus quickly translate increased nutrient uptake into growth, allowing it to outcompete other slower-growing species, such as *Ledum palustre,* which showed reduced growth in response to added snow. Two grasses, *Eriophorum angustifolium* and *E. vaginatum,* also showed

enhanced growth under snow addition, and increases in both C and N pools, providing further evidence that deeper snow increases the nutrients available for plant uptake. For *L. palustre* and others that showed either minimal increases or reduced growth responses, negative effects of added snow, such as a shorter growing season or delayed phenology, likely outweighed positive aspects of increased snow. Overall, plants that were able to translate increased nutrients into rapid and efficient growth performed best and will likely dominate the ecosystem if the simulated conditions become reality.

Our results provide evidence that deciduous shrubs will continue to expand in cover across the Arctic under this climate change scenario. Our work offers important insight into the ecosystem changes that are likely to occur if deciduous shrubs dominate the landscape and other species decrease in abundance. Perhaps one of the most important ways increased shrub cover is likely to change ecosystem functioning is through changes in nutrient cycling. We've shown that secondary growth (wood production) is an important way by which shrubs can increase their growth. Since wood is composed primarily of C-rich compounds (Chapin 1980, 1989), we can expect substantial C storage in the stems of shrubs, which could result in net ecosystem carbon storage, and act as a negative feedback to climate change. However, litter composition will also change as shrubs continue to increase in abundance; both slowly-decomposing wood and quickly-decomposing leaves will increase as litter inputs, and depending on the relative abundance of each, will either result in slower or faster decomposition rates, respectively (Hobbie and Gough 2002, Cornelissen et al. 2007, Buckeridge et al. 2009). It seems unlikely that either C storage in stems or slower decomposition rates due to increases in woody litter components would counteract the effects of greatly increased annual leaf litter inputs from deciduous shrubs, resulting in overall net increases in decomposition rates and positively feeding back to climate change.

The physical structure of shrubs may also play a role in feedbacks to climate change. In the spring when snowmelt begins, increases in shrub canopy cover may reduce albedo, as dark material absorbs more heat than surrounding snow, and could negatively feed back into climate warming (Sturm et al. 2005, Chapin et al. 2005). Yet as

shrub patches both grow bigger and spread outward, facilitated by increases in secondary growth, they will shade the ground during the summer, which may result in cooler soil temperatures that could slow decomposition and permafrost thaw, both of which are negative feedbacks to climate change. It seems more likely though, that reduced surface albedo during spring melt-out may have disproportionately large benefits for shrub growth, compared to negative effects from shading, because heat absorption by green leaves will likely accelerate melt-out and lengthen the growing season, allowing for overall increased shrub productivity.

While the ways in which increased shrub cover can influence ecosystem processes are numerous, as demonstrated above, it seems likely that processes promoting shrub growth will prevail over those opposing shrub growth. This is evidenced by documented increases in shrub cover throughout the Arctic over the past several decades (e.g. Sturm et al. 2001, Tape et al. 2006, Myers-Smith et al. 2011) Such increases in productivity have been linked to climate change, specifically warmer air temperatures, but my work demonstrates that winter processes may also play an important role in facilitating shrub dominance in the Arctic, particularly through increases in wood production seen under increased snow conditions. In the past, wood production has been somewhat overlooked as an important aspect of growth, but we show that it is the necessary base for overall increases in shrub size, and is greatly enhanced by deeper snow.

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APPENDIX A: Supplementary material to chapter 2

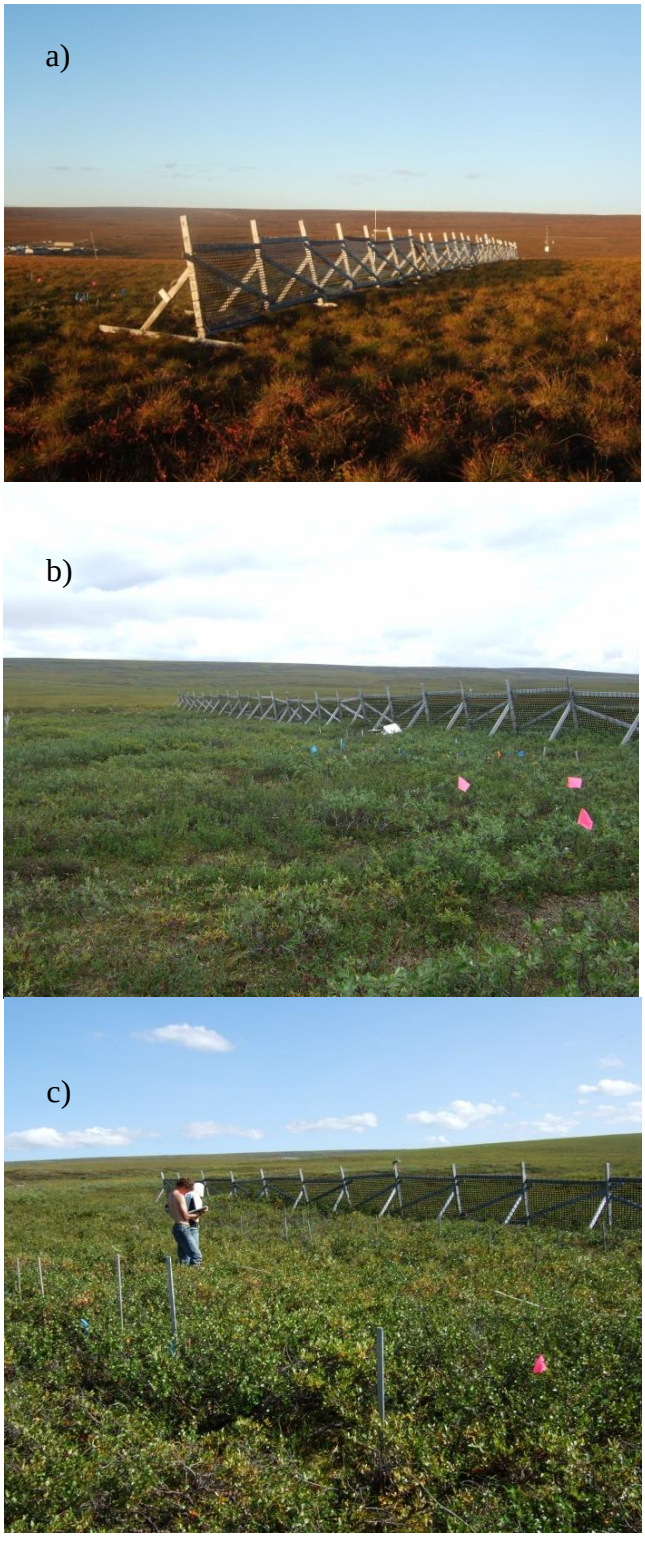

Figure A.1 Snow fences near Toolik Field station ranging in shrub height and density: a) low shrub, b) intermediate shrub, c) tall shrub.

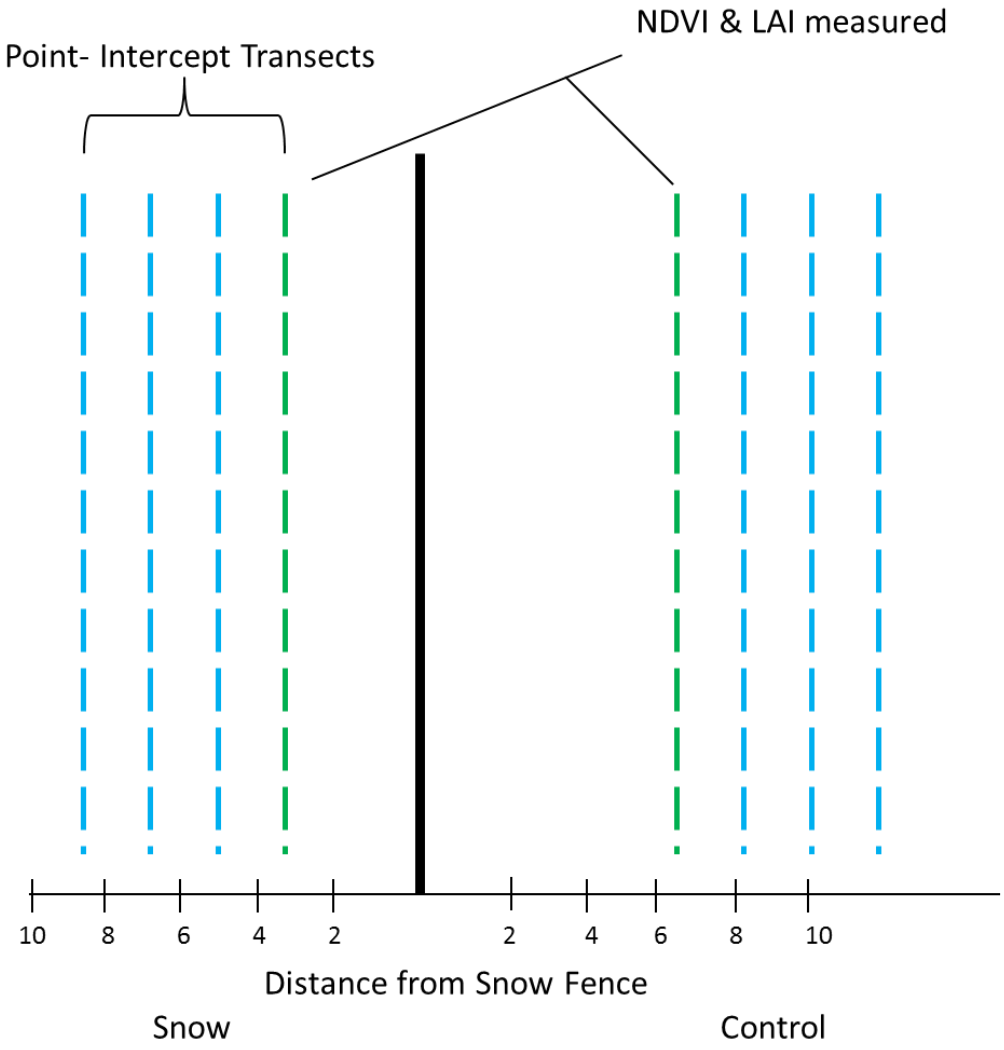

Figure A.2 Sampling design for the location of NDVI and LAI measurements, and point-intercept transects at each snow fence.

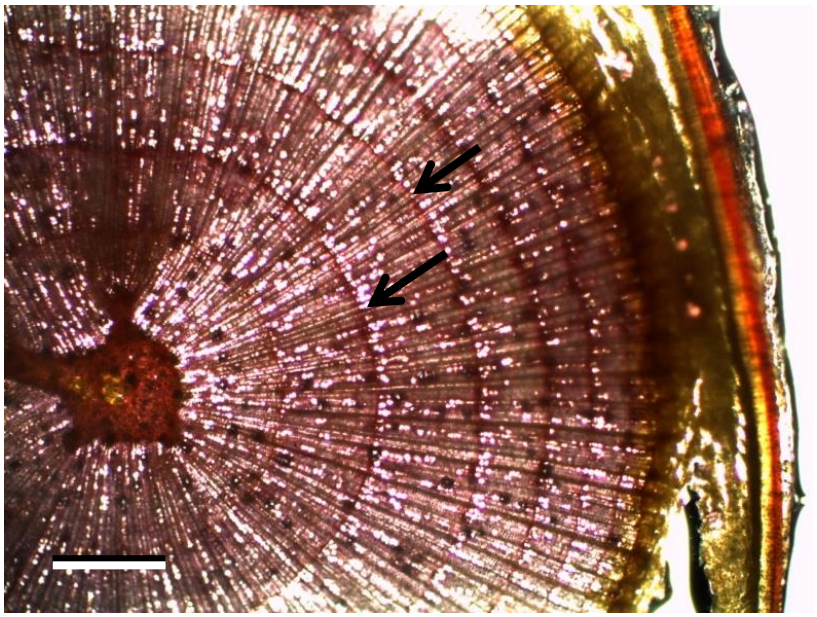

Figure A.3 Stained cross-section of a 6-year-old stem of *Betula nana*. Annual growth rings are indicated by black arrowheads. Bar = 300 µm.

Table A.1 Results of 2-way analysis of variance of growth traits of *Salix pulchra* by vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log-transformed where indicated in parentheses.

	Treatment (T)			Year (Y)			T x Y	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
Low shrub								
Total biomass	1,28	2.272 ns		1,28	3.855 ns		1,28	0.981 ns
Old stem biomass	1,28	1.713 ns		1,28	2.666 ns		1,28	1.680 ns
New stem biomass (rank)	1,28	**6.784***	S>C	1,28	**7.252***	'11<'10	1,28	0.499 ns
Leaf biomass	1,28	1.367 ns		1,28	4.180 ns		1,28	0.070 ns
# of branches	1,28	0.369 ns		1,28	0.671 ns		1,28	0.369 ns
Sec. growth rate	1,28	**8.683****	S<C	1,28	1.253 ns		1,28	0.458 ns
# of leaves	1,28	0.149 ns		1,28	1.372 ns		1,28	0.365 ns
Leaf Area	1,28	2.254 ns		1,28	3.287 ns		1,28	0.082 ns
Intermediate shrub								
Total biomass (ln)	1,28	**12.479****	S>C	1,28	11.622**		1,28	**7.436***
Old stem biomass (ln)	1,28	**12.378****	S>C	1,28	**17.064*****		1,28	**10.778****
New stem biomass (ln)	1,28	**7.671****	S>C	1,28	**5.610***	'11>'10	1,28	2.352 ns
Leaf biomass	1,28	**10.388****	S>C	1,28	**9.441****	'11>'10	1,28	3.730 ns
# of branches	1,28	**15.374*****	S>C	1,28	**10.255****	'11>'10	1,28	**5.712***
Sec. growth rate (rank)	1,28	**15.906*****	S>C	1,28	**7.432***	'11<'10	1,28	**4.284***
# of leaves	1,28	**16.367*****	S>C	1,28	**11.833***	'11>'10	1,28	**4.783***
Leaf Area	1,28	**15.683*****	S>C	1,28	**5.629***		1,28	3.590 ns
Tall shrub								
Total biomass	1,28	2.428 ns		1,28	1.675 ns		1,28	0.055 ns
Old stem biomass	1,28	1.147 ns		1,28	2.456 ns		1,28	0.155 ns
New stem biomass	1,28	2.231 ns		1,28	0.052 ns		1,28	0.504 ns
Leaf biomass	1,28	**7.570***	S>C	1,28	0.484 ns		1,28	0.171 ns
# of branches	1,28	**4.753***	S>C	1,28	3.930 ns		1,28	0.206 ns
Sec. growth rate (rank)	1,28	3.247 ns		1,28	2.214 ns		1,28	0.006 ns
# of leaves	1,28	**5.882***	S>C	1,28	3.601 ns		1,28	0.710 ns
Leaf Area	1,28	**4.348***	S>C	1,28	0.442 ns		1,28	0.0004 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.2 Results of 1-way analysis of variance of growth traits of *Salix pulchra* at the intermediate site, by year. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment		
Growth trait	df[a]	F	Post-hoc
2010			
Total stem biomass	1, 14	0.584 ns	
Old stem biomass	1, 14	0.018 ns	
# of branches	1, 14	3.680 ns	
Sec. growth rate	1, 14	**14.355****	**S>C**
# of leaves	1, 14	**5.867***	**S>C**
2011			
Total stem biomass	1, 14	**11.995****	**S>C**
Old stem biomass	1, 14	**13.440****	**S>C**
# of branches	1, 14	**11.842****	**S>C**
Sec. growth rate	1, 14	1.744 ns	
# of leaves	1, 14	**11.388****	**S>C**

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.3 Results of 2-way analysis of variance of growth traits of *Betula nana* by year. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log-transformed where indicated in parentheses.

	Vegetation Type (V)			Treatment (T)			V x T	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
2010								
Total biomass (rank)	1,28	**8.518*****	**L<T**	1,28	1.158 ns		1,28	0.159 ns
Leaf biomass (rank)	1,28	**6.112****	**L<T**	1,28	2.045 ns		1,28	0.343 ns
# of leaves (ln)	1,28	2.785 ns		1,28	0.903 ns		1,28	0.397 ns
Leaf area (ln)	1,28	**6.643****	**L<T**	1,28	2.224 ns		1,28	0.479 ns
2011								
Total biomass (rank)	1,28	**29.604*****	**L<I<T**	1,28	2.9013		1,28	2.937 ns
Leaf biomass (rank)	1,28	**26.706*****	**L<I<T**	1,28	2.003 ns		1,28	**3.632***
# of leaves (ln)	1,28	**9.496*****	**L<I,T**	1,28	3.228 ns		1,28	**3.571***
Leaf area	Homogenity of variance violated, analyzed by site							

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.4 Results of 1-way analysis of variance of growth traits of *Betula nana* in 2011, by vegetation type. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment	
Growth trait	df[a]	F
Low shrub		
leaf biomass	1,14	0.612 ns
# of leaves	1,14	0.023 ns
Leaf area	1,14	3.600 ns
Intermediate shrub		
leaf biomass	1,14	3.616 ns
# of leaves	1,14	4.546 ns
Leaf area	1,14	3.256 ns
Tall shrub		
leaf biomass	1,14	0.010 ns
# of leaves	1,14	0.071 ns
Leaf area	1,14	0.024 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.5 Results of 2-way analysis of variance of growth traits of *Betula nana* by vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2010, '10-2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log-transformed where indicated in parentheses.

	Treatment (T)			Year (Y)			T x Y	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
Low shrub								
Sec. growth rate	1,28	0.100 ns		1,28	1.487 ns		1,28	0.061 ns
# of leaves	1,28	.0004 ns		1,28	**5.197***	**'11>'10**	1,28	0.078 ns
Leaf area	1,28	2.419 ns		1,28	**4.652***		1,28	1.581 ns
Intermediate shrub								
Sec. growth rate (rank)	1,28	**9.389****	**S<C**	1,28	4.054 ns		1,28	0.375 ns
# of leaves (ln)	1,28	1.793 ns		1,28	**9.666****	**'11>'10**	1,28	**9.065****
Leaf area	1,28	1.974 ns		1,28	**9.625****	**'11>'10**	1,28	**4.297***
Tall shrub								
Sec. growth rate (rank)	1,28	2.282 ns		1,28	**14.435*****	**'11<'10**	1,28	1.014 ns
# of leaves	1,28	0.301 ns		1,28	**5.273***	**'11>'10**	1,28	0.035 ns
Leaf area	1,28	0.600 ns		1,28	**7.181***	**'11>'10**	1,28	0.299 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.6 Results of 1-way analysis of variance of growth traits of *Betula nana* at the intermediate site, by year. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment	
Growth trait	df[a]	F
2010		
# of leaves	1,14	1.614 ns
Leaf area	1,14	1.566 ns
2011		
# of leaves	1,14	4.546 ns
Leaf area	1,14	3.256 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.7 Results of 1-way analysis of variance of growth traits of *Ledum palustre*, *Vaccinium uliginosum*, and *Arctagrostis latifolia*, by year. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank or log-transformed where indicated in parentheses.

	Treatment		
Growth trait	df[a]	F	Post-hoc
Ledum palustre			
2010			
New stem biomass	1, 14	**17.266*** **	**S<C**
Sec. growth rate	1, 14	**10.293** **	**S<C**
# of branches	1, 14	0.84 ns	
2011			
New stem biomass	1, 14	0.028 ns	
Sec. growth rate (rank)	1, 14	**42.666*** **	**S<C**
# of branches (rank)	1, 14	0.691 ns	
Vaccinium uliginosum			
Leaf biomass 2010	1, 14	1.078 ns	
Leaf biomass 2011	1, 14	1.899 ns	
Arctagrostis latifolia			
Specific leaf area 2010	1, 14	0.049 ns	
Specific leaf area 2011 (rank)	1, 14	1.657 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.8 Results of 2-way analysis of variance of growth traits of *Eriophorum angustifolium* by vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2010, '10-2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment (T)			Year (Y)			T x Y	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
Intermediate shrub								
Leaf area	1, 28	**16.228*** **	**S>C**	1, 28	**5.209***	**'11<'10**	1, 28	1.166 ns
Tall shrub								
Leaf area	1, 28	0.015 ns		1, 28	**11.087****	**'11<'10**	1, 28	3.646 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table A.9 Results of 2-way analysis of variance of growth traits of *Eriophorum angustifolium* by year. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, I=intermediate site, T=tall site. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were log-transformed where indicated in parentheses.

	Vegetation Type (V)			Treatment (T)			V x T	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
2010								
Mass/tiller	1, 28	**29.048*** **	**I<T**	1, 28	**4.559***	**S>C**	1, 28	0.162 ns
Leaf area	1, 28	**24.631*** **	**I<T**	1, 28	4.087 ns		1, 28	0.003 ns
2011								
Mass/tiller	1, 17	**18.793*** **	I<T	1, 17	1.885 ns		1, 17	**6.052***
Leaf area (ln)	1, 28	**12.944****		1, 28	0.005 ns		1, 28	**8.758****

[a] Degrees of freedom are reported as (df treatment, df error)

Table A. 10 Results of 1-way analysis of variance of growth traits of *Eriophorum angustifolium* by vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment		
Growth trait	df[a]	F	Post-hoc
Intermediate shrub			
Mass/tiller 2010	1, 14	**6.940***	**S>C**
Mass/tiller 2011	1, 12	1.530 ns	
Leaf area 2011	1,14	7.136*	**S>C**
Tall shrub			
Mass/tiller 2010	1, 14	1.806 ns	
Mass/tiller 2011	1, 5	2.749 ns	
Leaf area 2011	1,14	3.844 ns	

[a] Degrees of freedom are reported as (df treatment, df error)

APPENDIX B: Supplementary Material to Chapter 3

Table B.1 Results of 2-way analysis of variance of nutrient pools of *Salix pulchra* by vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control, '11=2011, '10=2010. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were log-transformed where indicated in parentheses.

	Treatment (T)			Year (Y)			T x Y	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
Low shrub								
Total N pool	1, 28	1.842 ns		1, 28	4.102 ns		1, 28	0.613 ns
New stem N pool		not analyzed						
Leaf N pool	1, 28	0.947 ns		1, 28	1.526 ns		1, 28	0.113 ns
Total C pool	1, 28	2.284 ns		1, 28	3.409 ns		1, 28	0.997 ns
Old stem C pool	1, 28	1.532 ms		1, 28	2.113 ns		1, 28	1.472 ns
New stem C pool		not analyzed						
Leaf C pool	1, 28	1.305 ns		1, 28	3.705 ns		1, 28	0.066 ns
Old stem CN	1, 27	**6.126***	**S>C**	1, 27	2.81 ns		1, 27	0.15 ns
New stem CN		not analyzed						
Intermediate shrub								
Total N pool	1, 28	**8.404****	**S>C**	1, 28	**14.16*****	**'11>'10**	1, 28	**5.33***
New stem N pool	1, 28	**5.554***	**S>C**	1, 28	**5.591***	**'11>'10**	1, 28	1.987 ns
Leaf N pool	1, 28	**9.313****	**S>C**	1, 28	**14.16*****	**'11>'10**	1, 28	3.416 ns
Total C pool (ln)	1, 28	**12.581****	**S>C**	1, 28	**13.82*****	**'11>'10**	1, 28	**7.565***
Old stem C pool (ln)	1, 28	**12.646****	**S>C**	1, 28	**19.654*****	**'11>'10**	1, 28	**11.379****
New stem C pool (ln)	1, 28	**7.481***	**S>C**	1, 28	**6.26***	**'11>'10**	1, 28	2.414 ns
Leaf C pool	1, 28	**10.191****	**S>C**	1, 28	**10.555****	**'11>'10**	1, 28	3.447 ns
Old stem CN	1, 28	**15.723*****	**S>C**	1, 28	**16.325*****	**'11>'10**	1, 28	2.116 ns
New stem CN	1, 25	3.824 ns		1, 25	0.757 ns		1, 25	0.001 ns
Tall shrub								
Total N pool	1, 28	3.264 ns		1, 28	0.884 ns		1, 28	0.025 ns
New stem N pool	1, 28	2.221 ns		1, 28	0.132 ns		1, 28	0.634 ns
Leaf N pool	1, 28	**7.695****	**S>C**	1, 28	1.935 ns		1, 28	0.18 ns
Total C pool	1, 28	2.332 ns		1, 28	2.23 ns		1, 28	0.089 ns
Old stem C pool	1, 28	1.08 ns		1, 28	2.927 ns		1, 28	0.19 ns
New stem C pool	1, 28	2.024 ns		1, 28	0.18 ns		1, 28	0.377 ns
Leaf C pool (ln)	1, 28	**8.078****	**S>C**	1, 28	0.975 ns		1, 28	0.12 ns
Old stem CN	1, 28	0.098 ns		1, 28	24.03***	**'11>'10**	1, 28	1.531 ns
New stem CN	1, 24	0.376 ns		1, 24	4.037 ns		1, 24	0.013 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table B.2 Results of 1-way analysis of variance of nutrient pools of *Salix pulchra* at the intermediate site, by year. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment		
Growth trait	df[a]	F	Post-hoc
2010			
Total N pool	1, 14	0.639 na	
Total C pool	1, 14	0.602 ns	
Old stem C pool	1, 14	0.013 ns	
2011			
Total N pool	1, 14	**7.894***	**S>C**
Total C pool	1, 14	**11.747****	**S>C**
Old stem C pool	1, 14	**13.237****	**S>C**

[a] Degrees of freedom are reported as (df treatment, df error)

Table B.3 Results of 2-way analysis of variance of leaf C pool of *Betula nana* by year. Post-hoc tests indicate the direction of significant differences: L=low site, I=intermediate site, T=tall site. ***P<0.001, **P<0.01, *P<0.05, ns non-significant. Data were rank-transformed where indicated in parentheses.

	Vegetation Type (V)			Treatment (T)			V x T	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
Leaf C pool 2010 (rank)	2, 42	6.465**	L<T	1, 42	1.71 ns		2, 42	0.783 ns
Leaf C pool 2011 (rank)	2, 42	**26.434*****		1, 42	1.742 ns		2, 42	**3.792***

[a] Degrees of freedom are reported as (df treatment, df error)

Table B.4 Results of 1-way analysis of variance of leaf C pool of *Betula nana* in 2011, by vegetation type. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment	
Growth trait	df[a]	F
Leaf C pool		
low shrub	1, 14	0.716 ns
intermediate shrub	1, 14	3.762 ns
tall shrub	1, 14	0.003 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table B.5 Results of 2-way analysis of variance of tiller nutrient pools of *Eriophorum angustifolium* by vegetation type. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment (T)			Year (Y)			T x Y	
Growth trait	df[a]	F	Post-hoc	df[a]	F	Post-hoc	df[a]	F
Intermediate shrub								
Tiller N pool	1, 25	**20.523*** **	**S>C**	1, 25	0.037 ns		1, 25	0.117 ns
Tiller C pool	1, 25	**17.573*** **	**S>C**	1, 25	0.771 ns		1, 25	0.015 ns
Tall shrub								
Tiller N pool	1, 19	0.0006 ns		1, 19	0.184 ns		1, 19	3.951 ns
Tiller C pool	1, 19	0.241 ns		1, 19	0.661 ns		1, 19	**5.01***

[a] Degrees of freedom are reported as (df treatment, df error)

Table B.6 Results of 1-way analysis of variance of tiller C pool of *Eriophorum angustifolium* by vegetation type. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment	
Growth trait	df[a]	F
Tiller C pool 2010	1, 14	2.63 ns
Tiller C pool 2011	1, 5	2.852 ns

[a] Degrees of freedom are reported as (df treatment, df error)

Table B.7 Results of 1-way analysis of variance of nutrient pools of *Ledum palustre*, and *Vaccinium uliginosum* by year. Post-hoc tests indicate the direction of significant differences: S=snow, C=control. ***P<0.001, **P<0.01, *P<0.05, ns non-significant.

	Treatment		
Growth trait	df[a]	F	Post-hoc
Ledum palustre			
2010			
Total N pool	1, 14	4.511 ns	S>C
CN stems	1, 9	**12.796****	S<C
2011			
Total N pool	1, 14	0.288 ns	
CN stems	1, 12	0.245 ns	
Vaccinium uliginosum			
2010			
N pool leaves	1, 14	1.261 ns	
C pool leaves	1, 14	1.256 ns	
2011			
N pool leaves	1, 14	3.818 ns	S<C
C pool leaves	1, 14	3.648 ns	S<C

[a] Degrees of freedom are reported as (df treatment, df error)